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# A REVISION OF THE MILLIPED GENUS *DICELLARIUS* WITH A REVALIDATION OF THE GENUS *THRINAXORIA* (POLYDESMIDA: XYSTODESMIDAE)

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*Abstract.*—The milliped genus *Dicellarius* consists of the valid species *okefenokensis* (Chamberlin), *atlanta* (Chamberlin), *sternolobus* Loomis, *bimaculatus* (McNeill), and *talapoosa* (Chamberlin), the last two of which are divided into three and two subspecies, respectively. The genus *Thrinaxoria* is revived to accommodate *lampra* (Chamberlin) and *bifida* (Wood). The other two species, *dela* and *leiacantha,* both authored by Chamberlin, are relegated to the synonymy of *D. bimaculatus fictus* (Chamberlin). The seven species are distinguished chiefly by details of the male gonopods, particularly the configurations of the distal elements, but the enlarged pregonopodal sternal lobes distinguish *sternolobus.* Females can also be determined to genus because the two species of *Thrinaxoria* have a receptacle or remnant thereof on the cyphopods, whereas *Dicellarius* lacks this structure. *Dicellarius* is centered in the Gulf Coastal Plain and spreads inland into the southern extremities of the Blue Ridge, Ridge and Valley, and Applachian Plateau Provinces. *Thrinaxoria* occupies a more northern and western area, ranging from northwestern Louisiana to southwestern North Carolina, and extending southward into the Coastal Plains of Georgia and Alabama. The two species of *Thrinaxoria* are allopatric and separated by over 100 miles. However, specific ranges overlap to a high degree in *Dicellarius,* and only *okefenokensis* is allopatric. *Dicellarius* consists of two lineages, one leading to *talapoosa* and *atlanta,* and the other to *bimaculatus, okefenokensis,* and *sternolobus.* Relationships between the three genera in the tribe Pachydesmini are presently unresolved. A new diagnosis is presented for the tribe to reflect improved knowledge of *Dicellarius* and resurrection of *Thrinaxoria.*

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The Gulf Coastal Plain of the southeastern United States is the center of abundance of the milliped tribe Pachydesmini. Two of the component genera, *Pachydesmus* and *Dicellarius,* are the dominant xystodesmids in lowland areas of Mississippi, Alabama, the Florida panhandle, and southern Georgia. *Pachydesmus* has traversed the Mississippi and Tennessee Rivers occurring in northern Louisiana and central Tennessee, but these waterways are distributional barriers for *Dicellarius. Pachydesmus* contains the largest American polydesmoids, which grow to over four inches in length, but the forms of *Dicellarius* are only a couple of inches long and equivalent in size to most apheloriine diplopods, though much stiffer. The two taxa possess common anatomical features whose significance was first recognized by Hoffman (1958), and in 1979 he formally united them in the tribe Pachydesmini.

The taxonomy of *Pachydesmus* is stable. It was revised by Hoffman (1958), and Shelley and Filka (1979) reported new distributional records and gonopodal variants of *P. crassicutis incursus* Chamberlin. The same cannot be said of *Dicellarius,* however. Its taxonomy is highly confused, and specific names cannot be assigned with any degree of confidence. As with most Nearctic diplopod genera, the existing literature on *Dicellarius* consists of short, vague descriptive accounts accompanied by meaningless illustrations. None of its species has been adequately characterized, and only one, *sternolobus* Loomis, was assigned to *Dicellarius* in its original proposal. The generic validation, moreover, was a single sentence in a paper on other millipeds, so *Dicellarius* has not received a word of diagnosis. Thus, a revision of this genus is needed to stabilize its nomenclature and redescribe the component species, so that the millipeds can be used in field and experimental research in other biological disciplines.

One of the first observations engendered by this study is that *Dicellarius,* as envisioned by Hoffman (1979), is heterogeneous. The Louisiana species formerly in *Thrinaxoria, D. lampra* (Chamberlin), is unique in having a sharp caudal bend on the gonopodal acropodite such that the distal elements, widely separated in this species, are discontinuous with the axis. In contrast to the other species, females of *D. lampra* possess a receptable on the cyphopods, and there is an allopatric eastern form in which both the receptacle and the bend of the acropodite are reduced. The eastern form, occurring in Tennessee, North Carolina, and Georgia, also differs in having a generally longer prefemoral process that is parallel to the acropodite in medial view, as opposed to the Louisiana populations in which the structure angles across the acropodite stem. The magnitude of these and other differences suggests that the two forms are reproductively isolated and that *Thrinaxoria* should be resurrected to accommodate them. Their removal from *Dicellarius* leaves it with a more homogeneous content and results in two generic segregates with comparable differences between their component species. As a consequence of this change and from improved anatomical knowledge of all the species, alterations are necessary in Hoffman's diagnosis (1979:187) of the tribe Pachydesmini. The species of both *Dicellarius* and *Thrinaxoria* lack coxal apophyses, which are therefore an apomorphic feature of *Pachydesmus.* The transverse sternal ridges called "podosterna" for *Pachydesmus* (Hoffman 1958) are reduced and sometimes barely detectable in both *Dicellarius* and *Thrinaxoria,* so their usage as a primary tribal character should be qualified. Hence, I also include a revised diagnosis of this tribe, whose chief features are gonopodal.

The realization that *Thrinaxoria* is a valid genus comprised of two species affords the opportunity to resolve an outstanding enigma in diplopodology and assign the name *Polydesmus bifidus* Wood, heretofore regarded unofficially as a nomen inquirendum. In transferring *bifidus* to *Epeloria,* Chamberlin and Hoffman (1958) predicted that it might be a form of *Thrinaxoria,* and this prophecy can now be confirmed. The types of this species are lost, and Wood's original description and illustration (1864, 1865) do not clearly indicate the identity of the form(s) under study. However, he had material from both Georgia and Texas, which corresponds closely to the known range of *Thrinaxoria,* since *lampra* probably occurs in the northeastern corner of Texas (see species account). Wood's illustration of the *bifidus* gonopod is also very similar to the in situ configuration of the two species of *Thrinaxoria* (compare with Fig. 25), so I think he had both forms on hand and assumed they were conspecific. Wood did not give precise localities for his material, only the states of Georgia and Texas. However, the Georgia sample was probably from the mountains of north Georgia since the eastern species of *Thrinaxoria* is more common in this section of the state (see Fig. 29). Wood did not indicate which sample he considered the types, so his name could be assigned to either species of *Thrinaxoria.* However, since *lampra* is available for the western species, both names are conserved by assigning *bifida* to the eastern one and changing the gender of the suffix. This resolution is also compatible with the law of priority, which does not apply here, since Georgia precedes Texas in Wood's accounts. In the absence of his material, I designate a neotype for *bifida* from Polk County, Tennessee, which is adjacent to Fannin and Murray counties, Georgia, and the only county where more than one male has been collected.

As with *P. bifidus,* the type specimens of *Fontaria lamellidens* Chamberlin are also lost. However, Chamberlin (1931) reported a precise type locality, Biloxi, Harrison County, Mississippi, and the identity of this nominal species can be determined from near topotypical material. My analysis indicates that *F. lamellidens* is a race of *D. bimaculatus* (McNeill).

In the *Dicellarius* section of this paper, I depart from my usual practice of describing the type-species and comparing and contrasting the others with it. The type-species of *Dicellarius, D. okefenokensis* (Chamberlin), is atypical in its small size and gonopodal torsion, and I have therefore chosen *D. bimaculatus* as the basis for anatomical comparisons in this genus. I also show only the medial aspect of the gonopods of most forms because the prefemoral process is masked in lateral view and the positions of the solenomerite and tibiotarsus are merely reversed. This study indicates that *Dicellarius* consists of five valid species, two of which have recognizable geographic races, and that *Thrinaxoria* is comprised of two species. Information on variation and distribution is presented in the species or subspecies accounts along with appropriate synonymies. Acronyms of sources of preserved study material are as follows:

AU—Department of Zoology and Entomology, Auburn University, Auburn, Alabama.

CC—Biology Department, Columbus College, Columbus, Georgia.

FSCA—Florida State Collection of Arthropods, Gainesville, Florida.

MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

MEM—Mississippi Entomological Museum, Mississippi State University, Starkville, Mississippi.

NCSM—North Carolina State Museum of Natural History, Raleigh, North Carolina. The invertebrate catalog numbers of material in this institution are indicated in parentheses.

NMNH—National Museum of Natural History, Smithsonian Institution, Washington, D.C.

RLH—Private collection of Richard L. Hoffman, Radford, Virginia.

RVC—Private collection of the late Ralph V. Chamberlin, now being accessioned by the NMNH.

UMMZ—Museum of Zoology, University of Michigan, Ann Arbor, Michigan.

WAS—Private collection of William A. Shear, Hampden-Sydney, Virginia.

## Literature Review

The genus *Dicellarius* was established incidentally by Chamberlin (1920) in the introduction to a paper describing a new species of *Eurymerodesmus.* It was mistakenly assigned to the family Leptodesmidae, now a synonym of Chelodesmidae. The single sentence proposing the taxon reads, "The second (new North American leptodesmid genus) may bear the name *Dicellarius,* with *Leptodesmus okefenokensis* Chamberlin the genotype." According to the International Commission of Zoological Nomenclature, this pre-1931 statement validates *Dicellarius* because it was published in combination with an indication, an available specific name. Thus, *Dicellarius* is the oldest genus-group name for forms referrable to *Epeloria* and *Spathoria,* and must be retained in modern xystodesmid taxonomy even though no diagnostic statements have ever been published. Its type-species was described by Chamberlin (1918) from Billy's Island in the Okefenokee Swamp, Georgia.

Chamberlin (1931) proposed *Fontaria lamellidens* from Biloxi, Mississippi, and (1939) designated it the type of the new genus *Spathoria. Polydesmus bimaculatus,* described by McNeill (1887) from Pensacola, Florida, was transferred into *Spathoria* as the other component species. Chamberlin (1939) also erected *Epeloria* for the new species *E. talapoosa,* misspelling the type locality, Tallapoosa, Georgia, in both the locality citation and the specific name. Since the name was misspelled in both places, it cannot be considered an emendable lapsus, and the error must be retained in modern nomenclature.

During the 1940's, Chamberlin named five new species of *Epeloria* as follows: *fictus* (1943), *dela* and *leiacantha* (1946a), *atlanta* (1946b), and *nannoides* (1949). Chamberlin and Hoffman (1950) erected *Thrinaxoria* for *Fontaria lampra* Chamberlin, listing *Zinaria aberrans* Chamberlin as a synonym. These two nominal species were described from Louisiana by the author in 1918 and 1942, respectively. During this period new locality records of *E. leiacantha* were reported by Chamberlin (1947, 1951), and Causey (1955) published the first Florida locality of *E. fictus.* Causey also transferred *bimaculatus* into *Epeloria* from *Spathoria* and reported new localities for this species from Alabama and Mississippi. Chamberlin and Hoffman (1958) recognized three genera in their checklist–*Dicellarius, Epeloria,* and *Thrinaxoria*–and assigned *Spathoria* to synonymy under *Dicellarius.* Thus *Dicellarius* consisted of *okefenokensis,* the type-species; *bimaculatus,* transferred from *Epeloria*; and *lamellidens,* referred there because of the generic synonymy. They listed all the species under *Epeloria* that were then assigned to it except *nannoides,* which was synonymized with *D. okefenokensis,* and also brought *Polydesmus* (*Fontaria*) *bifidus* Wood into the genus, predicting that it might prove to be a form of *Thrinaxoria.* Thus *Epeloria* included *talapoosa, dela, leiacantha, atlanta, ficta* and *bifida.* As in 1950, Chamberlin and Hoffman (1958) still considered *Thrinaxoria* to be monotypic, and they added Tuscaloosa, Alabama, as the second locality for *lampra.*

Since 1958 only two authors have dealt with *Dicellarius.* Loomis (1969) proposed *D. sternolobus* from Tallapoosa County, Alabama, and published a key distinguishing *bimaculatus, lamellidens, okefenokensis,* and *sternolobus,* the four species then in the genus. Hoffman (1979) placed *Epeloria, Thrinaxoria,* and *Spathoria* in synonymy under *Dicellarius* and formally proposed the tribe Pachydesmini for *Pachydesmus* and *Dicellarius.* He also stated that *Dicellarius* consisted of four species in the southeastern states, but since these were not mentioned specifically, the previous taxonomy still stands. Thus at this writing, *Dicellarius* consists of the following 11 species listed chronologically below with their type localities and other reported states of occurrence. Suffix endings have been changed to masculine where necessary for agreement in gender.

*D. bifidus* (Wood, 1864). Described from Georgia and Texas, no definite localities known.

*D. bimaculatus* (McNeill, 1887). Pensacola, Escambia Co., Florida; also reported from Mobile Co., Alabama, and Jackson Co., Mississippi.

*D. okefenokensis* (Chamberlin, 1918). Billy's Island, Okefenokee Swamp, Charlton Co., Georgia; also reported from Gainesville, Alachua Co., Florida.

*D. lamprus* (Chamberlin, 1918). Creston, Natchitoches Par., Louisiana; also reported from Shreveport, Caddo Par., Louisiana; and Tuscaloosa, Tuscaloosa Co., Alabama.

*D. lamellidens* (Chamberlin, 1931). Biloxi, Harrison Co., Mississippi.

*D. talapoosa* (Chamberlin, 1939). Tallapoosa, Haralson Co., Georgia.

*D. fictus* (Chamberlin, 1943). Thomasville, Thomas Co., Georgia; also reported from Tallahassee, Leon Co., Florida.

*D. delus* (Chamberlin, 1946). Morgan, Calhoun Co., Georgia, incorrectly reported as being in Morgan Co. by Chamberlin and Hoffman (1958).

*D. leiacanthus* (Chamberlin, 1946). Along Spring Cr., Decatur Co., Georgia; also reported from Ft. Benning, Muscogee-Chattahoochee cos., Georgia, and an unspecified county in Alabama.

*D. atlanta* (Chamberlin, 1946). Atlanta, Fulton-Dekalb cos., Georgia.

*D. sternolobus* Loomis, 1969. Alexander City, Tallapoosa Co., Alabama.

## Taxonomic Characters

The genera *Dicellarius* and *Thrinaxoria* can be distinguished in either sex. In females of the latter, the cyphopods possess a receptacle or remnant thereof, whereas this structure is absent in *Dicellarius*. In males of *Thrinaxoria* the solenomerite and tibial process of the acropodites, collectively referred to as "distal elements," arise near midlength, are widely separated, and never lie over one another in medial or lateral views. In *Dicellarius* the elements arise distal to the midlength, are moderately separated at best, and one is frequently obscured by the other in these perspectives. *Pachydesmus* differs from both these taxa in the large postgonopodal sternal elevations, the apophyses on the gonopodal coxae, and the proximal origin of the elements of the acropodite, which arise at the juncture with the prefemur.

In *Dicellarius,* body size is useful in distinguishing *D. okefenokensis,* since it is much smaller than any other congener. It is the only species whose adults are less than 30 mm long and 5 mm wide, and female only samples of *D. okefenokensis* and *D. b. fictus* can therefore be separated on this basis. The only other somatic features of taxonomic importance in *Dicellarius* are the pregonopodal sternal projections in *D. sternolobus.* Although variable, these structures are distinctly visible on segments 4 and 5, and are at least subequal in length to the widths of the adjacent coxae (Figs. 19–20). In all the other species, the processes are small and have no taxonomic value (Figs. 1–2).

The remaining taxonomic characters in *Dicellarius* are located on the gonopods.

Aspects that are important include the in situ configuration, the orientation of the prefemoral process, the general curvature and configuration of the acropodite, the course of the prostatic groove, and the shape of the distal elements.

In most forms the tips of the acropodites overlap in situ (Figs. 7, 13), and where they are far enough apart, the distal elements may crisscross (Fig. 15). In *D. atlanta* and *D. bimaculatus fictus,* however, the acropodites do not overlap but lie side by side in a subparallel arrangement (Figs. 5, 17), thus allowing distinction from the other forms.

The prefemoral process is acicular to some degree in most forms of *Dicellarius,* but it is directed differently due largely to the configuration of the acropodite. The process lies parallel to the acropodite stem (above in medial view) in many forms, but it may angle across the stem with the tip either lying over the far side or protruding beyond the opposite margin (Figs. 8, 14, 22). In *D. okefenokensis* and *D. bimaculatus fictus,* the acropodite curves subanteriad so that the distal elements overhang the level of the prefemoral process in the former (Fig. 10) and overlap the tip of the process in the latter (Fig. 6).

The prostatic groove is typically completely visible in medial view from its origin in the base of the prefemur to its termination at the tip of the solenomerite. In some forms, however, it meets the anterior margin at the base of the solenomerite, where it continues to the terminal opening (Fig. 14, 18). The extreme condition obtains in *D. okefenokensis,* where the groove crosses to the lateral side because of torsion in the acropodite (Figs. 10–12). This situation is convergent with torsion in the tribe Apheloriini, and represents a derived, autapomorphic trait in *D. okefenokensis.*

The configuration of the distal elements and their position relative to each other are very important in the identification of a species or subspecies of *Dicellarius.* They are at most only moderately separated, and either lie parallel to each other or diverge apically. Both structures may be visible in medial or lateral views, in which case the gap between them also shows (Fig. 18), or one may overlie the other, completely obscuring the gap and at least partly hiding the opposite member (Figs. 8, 10). The tibial process may be shorter or longer than the solenomerite, but it is never narrower and sometimes is considerably wider. The configuration of the solenomerite is the most reliable determinant of the highly variable species *D. bimaculatus.* Here the structure is parallel-sided except for the tip, where the outer edge angles abruptly toward the inner forming a subacuminate inner corner (Figs. 4, 6, 8). Another way of describing this condition would be to say that the inner corner is produced or elongated. By contrast, the solenomerite is acicular in *D. talapoosa, D. atlanta,* and *D. sternolobus,* and both sides taper smoothly and continuously throughout the length to a subacuminate tip located in the midline (Figs. 14, 16, 18, 22).

In *Thrinaxoria* the taxonomic characters involve the size of the receptacle on the cyphopods, the degree of bend on the acropodites, and the length and orientation of the prefemoral process. *Thrinaxoria lampra* has a moderate-size receptacle, whereas it is a remnant or vestige in *T. bifida.* The acropodites display a smoother curve in the latter species, and the distal elements are more or less continuous with the curvature. The prefemoral process in *T. lampra* is shorter than in *T. bifida* and always angles across the acropodite stem in medial view. In

*T. bifida,* however, the structure usually lies parallel to the acropodite and extends linearly along its anterior margin (Figs. 26, 28).

### Tribe Pachydesmini Hoffman

Pachydesmini Hoffman, 1979:158, 187.

*Components.*—*Pachydesmus* Cook, 1895; *Dicellarius* Chamberlin, 1920; *Thrinaxoria* Chamberlin and Hoffman, 1950.

*Diagnosis.*—Relatively stiff, inflexible Xystodesminae of small to large size; sterna broad, with or without variable, transversely oval ridges or elevations on midbody segments; gonopods small to large, with or without dorsal coxal apophysis, telopodite usually linear proximad, curving or bending distal to midlength, with long slender accessory process paralleling acropodite or with slender subterminal branch; cyphopods with or without receptacle or remnant thereof.

*Range.*—Southeastern United States, from the eastern edge of Texas to coastal Georgia, South Carolina, and the southcentral part of North Carolina (Piedmont Plateau) just north of the state line, ranging northward across Tennessee and southward into the central Florida peninsula.

*Remarks.*—This revised diagnosis incorporates several modifications necessitated by validation of *Thrinaxoria* and by improved knowledge of *Dicellarius.* It allows for the small size of *D. okefenokensis*; the absence of the coxal apophysis in all species of *Thrinaxoria* and *Dicellarius*; the reduced sternal ridges in both genera; and the variable condition of the receptacle on the cyphopods. These changes diminish the tribe's distinctiveness from the Apheloriini, over which it has taxonomic priority. An additional diagnostic phrase is therefore inserted on the generally linear telopodites, demonstrated by all species except *D. okefenokensis,* in which the broad curvature is clearly derived. This feature of the telopodites does distinguish the Pachydesmini from the Apheloriini, where as described by Hoffman (1979), the telopodites are either semicircular, sigmoidal, or are bent or curved strongly mesad. The date of proposal of *Dicellarius* is also corrected to 1920.

### Genus *Dicellarius* Chamberlin

*Dicellarius* Chamberlin, 1920:97.—Chamberlin and Hoffman, 1958:30.—Hoffman, 1979:158.
*Epeloria* Chamberlin, 1939:3; 1949:101.—Causey, 1955:24.—Chamberlin and Hoffman, 1958:32.
*Spathoria* Chamberlin, 1939:6.

*Type-species.*—Of *Dicellarius, Leptodesmus okefenokensis* Chamberlin, 1918, by original designation; of *Epeloria, E. talapoosa* Chamberlin, 1939, by original designation; of *Spathoria, Fontaria lamellidens* Chamberlin, 1931, by original designation.

*Description.*—A genus of small to moderately large xystodesmids with the following characteristics:

Body composed of head and 20 segments in both sexes; size varying from 4–

8.5 mm in width and 22–42 mm in length; W/L ratio similarly varying from about 17–22.5%.

Color in life variable; most forms with drab olive-brown base color, lighter margins, and darker stripes along caudal edges of metaterga.

Head of normal appearance, moderately smooth and polished, occasionally finely granulate. Epicranial suture distinct, terminating in interantennal region, not apically bifid; interantennal isthmus variable; genae not margined laterally, with variable central impressions, ends broadly rounded and projecting slightly beyond adjacent cranial margins. Antennae moderately slender, varying in length, becoming progressively more hirsute distally, with 4 conical sensory cones on ultimate article; no other sensory structures apparent. Facial setae with epicranial, frontal, genal, clypeal, and labral series; with or without interantennal and subantennal.

Terga usually smooth and moderately polished; becoming moderately coriaceous on paranota. Collum variable, ends subequal to or extending well beyond those of following tergite. Paranota moderately to strongly depressed, caudolateral corners rounded on anteriormost segments, becoming blunt in midbody regions and progressively more acute posteriorly. Peritremata distinct, strongly elevated above paranotal surface; ozopores located caudal to midlength, opening dorsad to dorsolaterad. Prozonites smaller than metazonites; strictures moderately distinct, slightly costulate.

Caudal segments normal for family.

Sides of metazonites variable, usually granulate, with or without shallow grooves and impressions. Gonapophyses broad, apically expanded. Pregonopodal sterna of males variously modified; that of segment 4 with minute projection, much shorter than widths of adjacent coxae, or large apically divided process, longer than widths of adjacent coxae; sternum of segment 5 with low, transverse ridge or large, ventrally directed process between anterior legs, latter much longer than widths of adjacent coxae, and with variable impressions between posterior legs; 6th sternum with variable impressions between caudal legs to accommodate apices of acropodites. Postgonopodal sterna mildly hirsute, with or without variable low, rounded, longitudinal or transverse elevations in midlines of midbody segments. Coxae without projections; prefemoral spines relatively long and sharply pointed; tarsal claws slightly bisinuate. Hypoproct broadly rounded; paraprocts with margins slightly thickened.

Gonopodal apertures ovoid to elliptical, with or without slight anteriolateral indentations, sides flush with or slightly elevated above metazonal surfaces. Gonopods in situ with apices overlapping, interlocking, or lying parallel to one another; usually with tips of prefemoral processes crossing. Coxae moderate in size, without apophyses, connected by membrane only, no sternal remnant. Prefemora moderate, with variable prefemoral processes arising on anterior or anteriomedial sides. Acropodites moderately thick and robust, well sclerotized; configurations variable, either extending sublinearly from prefemur or curving slightly anteriad; divided at around ⅔ length into solenomerite and tibial process, both variable in length, configuration, and position relative to the other. Prostatic grooves arising in pits in bases of prefemora, usually running entirely along medial sides of acropodite stems, crossing to anterior and lateral surfaces in some species; opening terminally on solenomerites.

Cyphopodal apertures elliptical, encircling 2nd legs, sides slightly elevated above metazonal surfaces, without pleurotergal lobes on anteriolateral corners. Cyphopods in situ located lateral to 2nd legs, variably positioned in apertures; without receptacles. Valves moderate to large, subequal, surfaces finely granulate. Opercula relatively large, located on lateral sides of valves.

*Distribution.*—Coastal Plain of Georgia, Florida, Alabama, and Mississippi; southern Ridge and Valley and Appalachian Plateau Provinces of Alabama; Piedmont Plateau and southern fringe of Blue Ridge Province of Georgia and North Carolina. The Tennessee River is a distributional barrier in northern Alabama, and the Savannah River forms the range limit along the Atlantic Coast.

*Species.*—Five, two of which are divided into two and three subspecies.

Key to species of *Dicellarius* (based primarily on adult males)

1. Body size small; acropodites with torsion, prostatic groove crossing from medial to lateral sides; tibial process overlying and largely obscuring solenomerite in medial view; southeastern Georgia to central Florida .... .......................................... *okefenokensis* (Chamberlin)
– Body size moderate; acropodites without torsion, prostatic groove either running entirely on medial side or angling to anteriomedial edge at midlength; distal elements variable in position and configuration, but tibial process never overlying solenomerite in medial view ................. 2
2. Sterna of segments 4 and 5 with large, ventrally directed processes, subequal to or longer than widths of adjacent coxae; solenomerite overlying tibial process in medial view, sides tapering smoothly and continuously to subacuminate tip; tibial process with several grooves and ridges on lateral surface; central Alabama ....................... *sternolobus* Loomis
– Sterna of segments 4 and 5 with at most minute projections, much smaller than widths of adjacent coxae; solenomerite variable, occasionally overlying tibial process in medial view and with sides parallel except apically; tibial process without noticeable ridges and grooves .................. 3
3. Tibial process broad, spatulate; sides of solenomerite parallel except apically, then narrowing abruptly to subacuminate tip on inner corner; central and eastern Georgia to western Florida, southern Alabama, and southern and eastern Mississippi .......................... *bimaculatus* (McNeill)
– Tibial process and solenomerite acicular, sides narrowing smoothly and continuously to subacuminate tips located in midlines ............... 4
4. Acropodite sublinear; distal elements subequal, moderately separated; prefemoral process on anterior side of acropodite; western North Carolina to central Georgia ..................................*atlanta* (Chamberlin)
– Acropodite curved gently caudad; distal elements contiguous to narrowly separated, solenomerite slightly longer; prefemoral process angling across stem of acropodite to caudal side; north-central Alabama to western Georgia ......................................... *talapoosa* (Chamberlin)

*Dicellarius bimaculatus* (McNeill)

*Diagnosis.*—Acropodite highly variable, either curved subanteriad, subcaudad, or submediad. Distal elements narrowly separated, continuing general curvature of acropodite, in some forms overlying one another in medial and lateral views; solenomerite laminate, sides parallel except at apex, then narrowing abruptly to subacuminate tip on inner corner; tibial process laminate and apically rounded, subequal in length to solenomerite.

*Remarks.*—*Dicellarius bimaculatus* is the widely-distributed species along the Gulf of Mexico occurring in the Coastal Plains of Georgia, Alabama, Mississippi, and the Florida panhandle. The type locality is Pensacola, Escambia County, Florida. Forms in the eastern ⅔ of the range demonstrate considerable gonopodal stability, but the incidence of variation rises around the Alabama and Escambia Rivers. Populations become increasingly more variable west of this point, and the gonopodal differences between forms at Mobile, Alabama, and Biloxi, Mississippi, a distance of about 45 miles, are much greater than the differences between forms at Savannah, Georgia, and Montgomery, Alabama, a distance of over 300 miles. The situation west of these rivers approaches a clinal transition, particularly along the Gulf Coast, and presents difficulties in making taxonomic decisions. The widespread, anatomically stable eastern form clearly represents a single geographic race, and three Chamberlinian names are available, the oldest being *D. b. fictus.* In the rest of the range, one could justifiably recognize one large, highly variable subspecies or a number of smaller, more stable ones. Two names have been proposed for forms from this area, *D. bimaculatus* the oldest one referable to the complex and hence the specific name, and *D. lamellidens* (Chamberlin). Thus, if subspecies are designated, the nominate will be from this area of anatomical instability. One alternative would be to include the form at Pensacola with the eastern one, enlarge its range slightly, and make it the nominate subspecies. However, I think that the stable eastern morphotype deserves recognition in its own right and that the nominate subspecies should therefore refer to another form. After analyzing males from every sample west of the Alabama and Escambia Rivers, it became evident that a single taxonomic unit could be described from all of this area except the coast of Mississippi. This entity becomes the nominate subspecies and is necessarily much more variable than *D. b. fictus.* However, the much greater variation along the coast of Mississippi clearly requires separate treatment. Since the name *lamellidens* is available, I propose a third subspecies with much smaller range west of the Pascagoula River. East of this boundary and in the city of Pascagoula the forms are intermediate between the "average" variant of *D. b. bimaculatus* and are thus considered intergrades. Other resolutions are possible, but this one maximizes the existing nomenclature and provides a balance between naming nearly every local population west of the Alabama and Escambia Rivers and ignoring subspecies altogether.

*Dicellarius bimaculatus bimaculatus* (McNeill), new status
Figs. 1–4

*Polydesmus bimaculatus* McNeill, 1887:323, figs. 3–5.
*Fontaria bimaculata.*—Attems, 1938:166.
*Spathoria bimaculata.*—Causey, 1955:24.
*Dicellarius bimaculatus.*—Chamberlin and Hoffman, 1958:30.

*Type specimens.*—Three male and 15 female syntypes (NMNH) collected by

C. H. Bollman, Mar–Apr 1886, at Pensacola, Escambia Co., Florida. I have designated one male as the lectotype.

*Diagnosis.*—Gonopods in situ with tips of acropodites curved slightly mediad and overlapping, prefemoral processes overlapping; prefemoral process narrow and acicular, tapering gradually distad, angling across acropodite stem and lying nearly entirely over latter in medial view; acropodite with curvature in medial plane and thus masked in medial view, extending sublinearly from prefemur; distal elements subequal in width and length, continuing linear configuration of acropodite; solenomerite with edge directed mediad.

*Lectotype.*—Length 31.3 mm, maximum width 6.3 mm, W/L ratio 20.1%, depth/width ratio 65.1%. Segmental widths as follows:

| | | | |
|---|---|---|---|
| collum | 4.9 mm | 5th–15th | 6.3 |
| 2nd | 5.4 | 16th | 5.8 |
| 3rd | 5.8 | 17th | 5.2 |
| 4th | 6.0 | 18th | 4.1 |

Color in life unknown. McNeill (1887) described the dorsum as being "obscure olive or chestnut, the scuta generally marked with an indistinct transverse dark band, with lighter color towards the margins; a well defined oval spot of gray is frequently present on the lateral margins; lateral laminae with a narrow pink border." This corresponds generally to my observations on living species of *Dicellarius.*

Head capsule smooth, polished; width across genal apices 3.3 mm, interantennal isthmus 1.4 mm; epicranial suture thin but distinct, terminating above interantennal region, not bifid. Antennae relatively short, reaching back only to middle of 3rd segment, becoming progressively more hirsute distally, first antennomere subglobose, 2–6 clavate, 7 short and truncate, relative lengths of antennomeres $2 > 6 > 3 > 4 > 5 > 1 > 7$. Genae not margined laterally, with distinct central impressions, ends broadly rounded and projecting slightly beyond adjacent margin of cranium. Facial setae as follows: Epicranial 2-2, interantennal absent, frontal 1-1, genal 3-3, clypeal about 14-14, labral about 20-20, merging with clypeal series and continuing for short distance along genal borders, about 3 setae on each side.

Terga smooth, polished, becoming moderately coriaceous on paranota. Collum broad, ends extending slightly beyond those of 2nd tergite. Paranota moderately depressed, continuing slope of dorsum, anterior corners blunt with distinct, elevated scapulorae, caudolateral corners rounded through segment 5, becoming blunt and progressively more acute posteriorly. Peritremata distinct, strongly elevated above paranotal surface. Ozopores located caudal to midlength of peritremata, opening dorsolaterad.

Sides of metazonites dull and granulate but without noticeable grooves or impressions. Strictures sharp, distinct, prozona elevated slightly above metazona. Gonapophyses broad, apically expanded. Pregonopodal sterna (Figs. 1–2) generally unmodified, without noticeable lobes or projections; 6th sternum recessed slightly between 7th legs to accommodate apices of acropodites. Postgonopodal sterna higher than prozonites, with transverse grooves between leg pairs merging into low, rounded, longitudinal elevations in midlines, elevations noticeable only on segments 8–15; caudal margins of sterna indented medially. Pregonopodal legs densely hirsute, postgonopodal legs becoming progressively less hirsute caudally. Coxae without projections; prefemoral spines beginning on segment 5, becoming longer and sharper on midbody region; tarsal claws faintly bisinuate. Hypoproct rounded, paraprocts with margins slightly thickened.

Gonopodal aperture 2.0 mm wide and 0.9 mm long at midpoint, indented slightly anteriolaterad, sides flush with metazonal surface. Gonopods in situ (Fig. 3, not this specimen) with acropodites projecting anteriad from aperture, extending well beyond anterior margin of aperture with tips overlapping between 7th legs, prefemoral processes also overlapping and extending beyond aperture. Gonopod structure as follows (Fig. 4): Prefemur moderate, with long acicular prefemoral process on anterior side angling over acropodite stem, bent anteriad distally and terminating just beyond base of tibial process, tip directed toward midlength of solenomerite. Acropodite curving submediad and curvature thus masked in medial view, projecting linearly from prefemur, sides narrowing gradually, divided at ¾ length into anterior solenomerite and posterior tibial process. Latter laminate, subequal in length to solenomerite, apically blunt. Solenomerite with sides subparallel except at apex, then narrowing abruptly to subacuminate tip on inner corner, curving broadly mediad with edge visible in medial view. Prostatic groove arising in pit in prefemur extending along medial surface of acropodite onto solenomerite, opening apically.

*Female paralectotype.*—Length 30.8 mm, maximum width 6.9 mm, W/L ratio 22.4%, depth/width ratio 63.8%. Agreeing closely with lectotype in most somatic features, except paranota more strongly depressed, giving appearance of more highly arched body, and sternal elevations greatly reduced, barely detectable.

Cyphopodal aperture elliptical, encircling 2nd legs, sides barely elevated above metazonal surface, without pleurotergal lobe on anteriolateral corners. Cyphopods in situ with valvular openings visible in aperture; valves large, subequal, surface finely granulate. Receptacle absent. Operculum relatively large, located on lateral side of valves, surface finely granulate.

*Variation.*—The length of the prefemoral process varies, and it does not extend to the level of the acropodite division in some males. It is always acicular, but does not always extend across the acropodite stem. In one male there is a small, subterminal spur. In all forms the acropodite curvature visible in situ (Fig. 3) is masked in medial view because it lies in the plane of vision and perpendicular to the plane of drawing. However, not all the acropodites are as straight as that of the lectotype. Some bend anteriad, as in *D. b. fictus,* while others tend to lean caudad. In the eastern part of the range the distal divisions appear as in the lectotype, but farther west in Mississippi they lean caudad and the anterior surface is seen in medial view. This variation befits the intermediate geographical position of *D. b. bimaculatus* between the other two subspecies.

*Distribution.*—Western Florida, southwestern and west-central Alabama, and east-central Mississippi. The Conecuh-Escambia River forms the approximate eastern boundary, but the western and northern extremes do not correspond with any physiographic features. Most localities are west of the Mobile-Tombigbee River. The subspecies is sympatric and syntopic with *T. lampra* in Washington

County, Alabama, along the Tombigbee River. Specimens were examined as follows:

FLORIDA: *Escambia Co.,* Pensacola, 3M, 15F, Mar–Apr 1886, C. H. Bollman (NMNH), F, Nov 1969, C. Seal (FSCA), and 3M, 7F, 15 Mar 1970, C. Seal (FSCA) TYPE LOCALITY; 3 mi. W Pensacola, 3M, F, 22 Jan 1965, N. B. Causey (FSCA); Atmore, 3M, F, 15 Mar 1962, C. R. Parker (FSCA); along US hwy. 90 E jct. FL hwy. 29, M, 1 Jan 1954, N. B. Causey (FSCA); Cantonment, M, 1 May 1954, N. B. Causey (FSCA); and 3 mi. SE Cantonment M, 25 Nov 1967, M. Tidwell (FSCA).

ALABAMA: *Monroe Co.,* 2.5 mi. E Chrysler, F, 18 Apr 1976, M. R. Cooper (NCSM A735); and 6 mi. S Monroeville, M, 10 Mar 1977, R. E. Woodruff (FSCA). *Conecuh Co.,* 0.8 mi. E Castleberry, along AL hwy. 6 at Murder Cr., M, 24 Apr 1983, R. M. Shelley and P. B. Nader (NCSM A4056); Evergreen, 3M, 10 Apr 1960, L. Hubricht (RLH); and 15 mi. N Evergreen, M, F, 9 Apr 1960, L. Hubricht (RLH). *Baldwin Co.,* Daphne, M, F, 14 Mar 1948, B. A. Maina (RLH); jct. US hwys. 90 & 98 W Loxley, 2F, 22 Jan 1955, N. B. Causey (FSCA). *Mobile Co.,* Spring Hill College, several MM, FF, 2 May 1954, C. E. Valentine (FSCA); Grand Bay, 4M, F, 17 Jun 1953, N. B. Causey (FSCA); Mobile, F, Apr 1954, N. B. Causey (FSCA); Theodore, M, 4F, 21 Jun 1961, L. Hubricht (RLH); 2.5 mi. SW Bucks, 2F, 13 May 1962, L. Hubricht (RLH); and along Alligator Cr. nr. Dog R., 2M, 3F, 21 Sep 1952, collector unknown (UMMZ). *Washington Co.,* 3 mi. E Leroy, 3 Jul 1960, L. Hubricht (RLH). *Clarke Co.,* Jackson, M, F, 23 Sep 1910, R. V. Chamberlin (RVC); Walker Springs, 2M, 25 Jul 1965, S. B. Peck (FSCA); and Coffeyville, F, 16 Jun 1959, N. B. Causey (FSCA). *Choctaw Co.,* E of Lavaca nr. Tombigbee R., M, F, 4 Jul 1960, L. Hubricht (RLH).

MISSISSIPPI: *Oktibbeha Co.,* State College, M, 19 Apr 1917, S. B. Pearce (MCZ); Craig Springs, 6M, F, 22 Apr 1980, and 3M, F, 15 May 1980, G. Snodgrass (MEM); and Starkeville, M, 14 May 1982, G. Sullivan (MEM). *Winston Co.,* Noxapater, 3 juvs., 29 Dec 1965, J. B. Black (FSCA). *Lauderdale Co.,* Meridian, 7M, F, 10 Dec 1961, L. Hubricht (RLH). *Jasper Co.,* Louin, 2M, 24 Mar 1963, L. Hubricht (RLH). *Wayne Co.,* 8 mi. E Waynesboro, 3M, 3F, 13 Mar 1963, L. Hubricht (RLH). *Jones Co.,* nr. Laurel, M, 2F, 15 Jul 1980, J. Robbins (MEM). *Lamar Co.,* Oak Grove, F, 12 Apr 1957, L. Smith (FSCA). *Forrest Co.,* Rawls Springs Twp. nr. Hattiesburg, M, 15 Feb 1957, B. D. Valentine (FSCA).

### *Dicellarius bimaculatus fictus* (Chamberlin), new combination, new status
Figs. 5–6

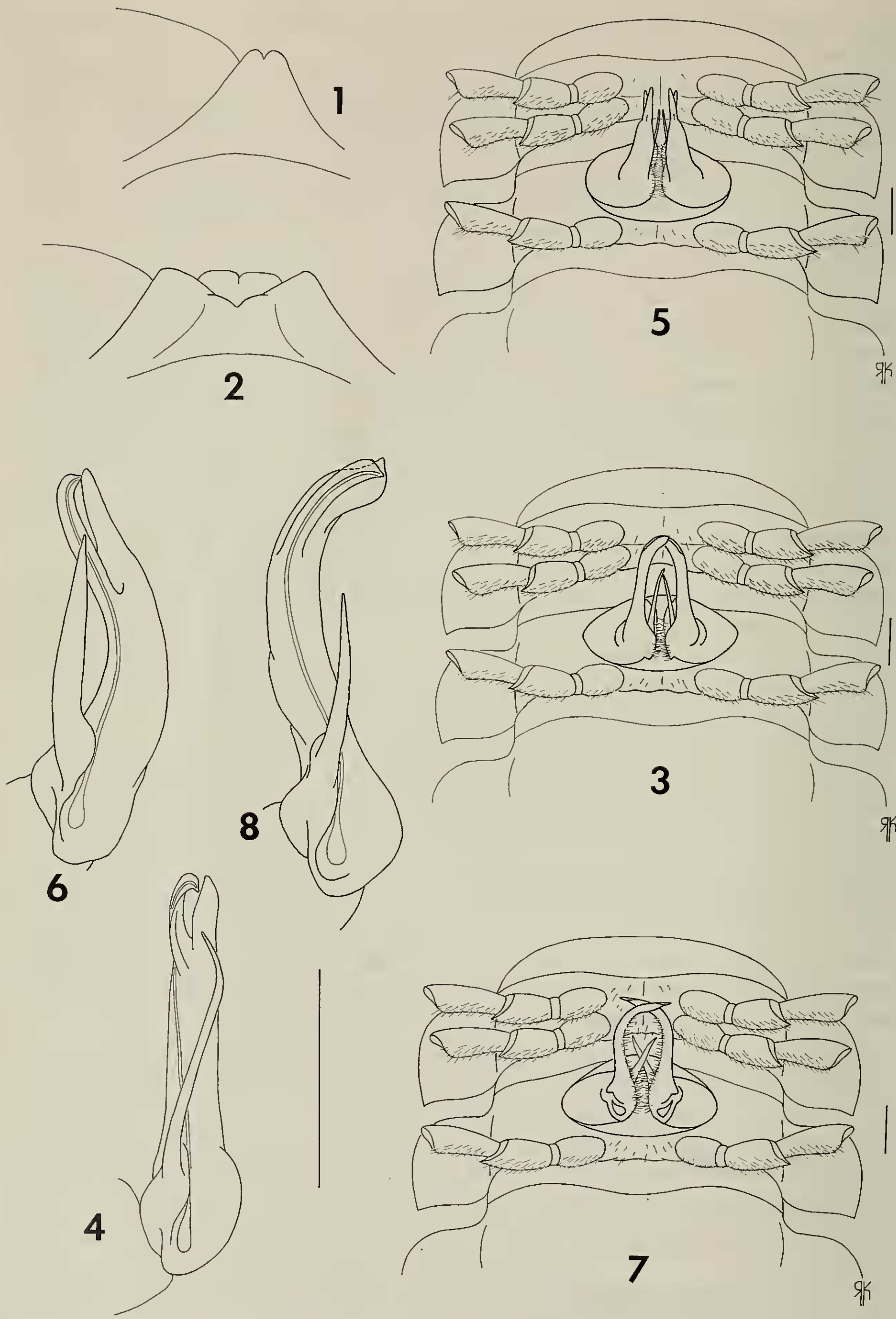
*Epeloria ficta* Chamberlin, 1943:37–38, fig. 11.—Chamberlin and Hoffman, 1958: 32–33.

*Epeloria fictus.*—Causey, 1955:24.

*Epeloria dela* Chamberlin, 1946a:139, figs. 1–2.—Chamberlin and Hoffman, 1958:32.

*Epeloria leiacantha* Chamberlin, 1946a:139–140, fig. 3; 1947:29; 1951:28.—Chamberlin and Hoffman, 1958:33.

*Type specimens.*—Male holotype and female allotype (RVC) collected by H. Field, 5–10 Apr 1940, from Thomasville, Thomas Co., Georgia.




Figs. 1–8. *Dicellarius bimaculatus*: 1–4, *D. b. bimaculatus.* 1, Sternum of segment 4 of lectotype, caudal view; 2, Sternum of segment 5 of the same, caudal view; 3, Gonopods in situ, ventral view of male from Lauderdale Co., MS; 4, Telopodite of left gonopod of lectotype, medial view; 5–6, *D. b. fictus.* 5, Gonopods in situ, ventral view of male from Grady Co., GA; 6, Telopodite on left gonopod

*Diagnosis.*—Gonopods in situ in subparallel arrangement, neither acropodites nor prefemoral processes overlapping; prefemoral process stout, wide basally and tapering sharply distad to acute tip, tip overlapping solenomerite; acropodite in medial view curved anteriad and extending over level of prefemoral process, distal elements subequal in width and length; solenomerite with profile visible in medial view.

*Variation.*—The acropodite configuration in this race is more stable than that of the nominate subspecies. All males display the diagnostic acropodal curvature, with the solenomerite, and also the tibial process in some individuals, overhanging the prefemoral process. The latter is the most variable gonopodal feature. It is usually a wide, straight spine as in the holotype, but it is bent distally in some individuals and apically bifurcate with a subterminal spur in others. The orientation of the solenomerite also varies so that the produced inner corner is visible medially in some males and not in others.

*Distribution.*—This subspecies has the widest distribution of any race of *D. bimaculatus,* and it is sympatric with *T. bifida* in Dougherty County, Georgia. The area includes the Fall Zone and Coastal Plain of Alabama east of the Tombigbee and Conecuh Rivers, the panhandle of Florida between the Blackwater and Suwannee Rivers, and the outer Piedmont Plateau and the Coastal Plain of Georgia except for the Suwannee River drainage in the southeastern corner. It abuts the ranges of *D. okefenokensis* in this area and *D. atlanta* and *D. talapoosa* in the north. A peripheral population in Chatham County, Georgia, is isolated from the rest of the range, although some of this hiatus may reflect inadequate collecting. The inner Coastal Plain has received little attention, and the Savannah record may connect with that in Tift County. Specimens were examined as follows:

GEORGIA: *Chatham Co.,* Savannah, Beaulieu Ave., 3M, F, 1 Nov 1959, L. Hubricht (RLH). *Chattahoochee Co.,* Ft. Benning, M, 16 Apr 1950, D. E. Beck (RVC); and along GA hwy. 137 at Bagley Cr., M, 5 Sep 1980, G. E. Stanton (CC). *Muscogee Co.,* Columbus College, M, F, 19 Oct 1977, G. E. Stanton (CC). *Lee Co.,* N of Albany, F, 18 Jun 1959, N. B. Causey (FSCA). *Tift Co.,* many MM and FF, Sep 1967–Oct 1968, J. A. Payne (RLH). *Dougherty Co.,* Albany, 2M, 12F, 12 Jun 1959, N. B. Causey (FSCA). *Calhoun Co.,* Morgan, M, 4 Apr 1946, P. W. Tratt (RVC); and Leary, M, 25 Mar 1961, L. Hubricht (RLH). *Early Co.,* between Saffold and Jakin, 2M, F, 18 Mar 1961, L. Hubricht (RLH); and Kolomoki Mounds St. Pk., 3M, 2F, 1 May 1983, R. M. Shelley and P. B. Nader (NCSM A4024). *Baker Co.,* Pineland Plantation nr. Newton, 3M, F, 30 Mar 1959, D. B. Jester and H. Wyatt (FSCA). *Seminole Co.,* 4.5 mi. SE Iron City, M, F, and Ray's Lake, F, 21 Mar 1954, T. H. Hubbell (UMMZ). *Decatur Co.,* Spring Cr. W of Brinson, 2M, 3 Apr and 20 Aug 1946, P. W. Fattig (RVC), 2M, 2F, 31 Mar 1964, H. W. Levi (MCZ), and several MM and FF, 26 Jan 1965, N. B. Causey (FSCA). *Grady Co.,* 3 mi. W Cairo, 4M, 6F, 26 Jan 1965, N. B. Causey

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of holotype, ventral view; 7–8, *D. b. lamellidens.* 7, Gonopods in situ, ventral view of male from Jackson Co., MS; 8, Telopodite of left gonopod of the same, medial view. Scale line for Figs. 3, 5, and 7 = 1.00 mm; line for other Figs. = 1.23 mm for 1 and 2; 1.00 mm for 4, 6, and 8. Setae are omitted from all dissected gonopod and sternal drawings in this paper.

(FSCA); and 8 mi. NE Cairo, along GA hwy. 188, M, 3F, 15 Sep 1979, R. M. Shelley and P. T. Hertl (NCSM A2875). *Thomas Co.,* Thomasville, M, F, 5–10 Apr 1940, H. Field (RVC) and 2M, 15 Jul 1973, W. A. Shear (WAS) TYPE LOCALITY; Bar-M-Ranch nr. Boston, 8M, 2F, Apr 1968, W. Sedgwick (WAS) and M, F, 15 Jul 1973, W. A. Shear (WAS). *Brooks Co.,* 8 mi. W Quitman, along US hwy. 84, F, 7 Jul 1960, N. B. Causey (FSCA).

ALABAMA: *Marengo Co.,* Chickasaw St. Pk., M, F, 15 Jun 1959, N. B. Causey (FSCA) and 4M, F, 8 Jul 1980, R. M. Shelley (NCSM A3350). *Dallas Co.,* Selma, 2M, 2F, 15 June 1959, N. B. Causey (FSCA). *Wilcox Co.,* nr. Camden, 4M, 2F, 11 Nov 1962, L. Hubricht (RLH); and 5 mi. W Snow Hill, M, 10 Apr 1960, L. Hubricht (RLH). *Lowndes Co.,* 2.5 mi. NE Sandy Ridge, F, 9 Apr 1960, L, Hubricht (RLH); and 8.4 mi. NE Ft. Deposit, 3M, F, 19 Apr 1983, R. M. Shelley and P. B. Nader (NCSM A4029). *Montgomery Co.,* 7 mi. SW Montgomery, 4M, 3F, 16 Apr 1960, L. Hubricht (RLH); and 13.1 mi SSW Montgomery, along US hwy. 31 nr. Pintlalla, M, F, 19 Apr 1983, R. M. Shelley and P. B. Nader (NCSM A4025). *Butler Co.,* McKenzie, M, F, 9 Apr 1960, L. Hubricht (RLH); 15.9 mi. NW Greenville, along AL hwy. 11, 0.2 mi. N jct. AL hwy. 54, 3M, 21 Apr 1983, R. M. Shelley and P. B. Nader (NCSM A4038); and 6 mi NE Searcy, 3M, F, 9 Apr 1960, L. Hubricht (RLH). *Macon Co.,* 11.9 mi. SW Tuskegee, M, 10 May 1973, R. B. Little (AU). *Crenshaw Co.,* Brantley, M, 17 Jul 1960, L. Hubricht (RLH); and Luverne, 4M, 19 Mar 1961, L. Hubricht (RLH). *Pike Co.,* 10.8 mi. NW Troy, M, 26 Apr 1983, R. M. Shelley and P. B. Nader (NCSM A4060). *Russell Co.,* 10.8 mi. SW Phenix City, 2M, 26 Apr 1983, R. M. Shelley and P. B. Nader (NCSM A4063). *Coffee Co.,* jct. US hwy. 84 and AL hwy. 87 nr. Elba, 2M, 8F, 26 Jan 1965, N. B. Causey (FSCA). *Geneva Co.,* 1 mi. E Geneva, along Choctawhatchee R., 2M, 2 Jul 1960, L. Hubricht (RLH); and 5.8 mi. S Hartford, M, 30 Apr 1983, R. M. Shelley and P. B. Nader (NCSM A4078). *Houston Co.,* 1 mi. SE Grangeburg, M, 26 Mar 1961, and 4.5 mi. W Avon, 3M, 18 Mar 1961, L. Hubricht (RLH); 4 mi. E Webb, along Cedar Spring Cr., 3M, 9 Jul 1967, D. R. Whitehead (RLH); and Chattahoochee St. Pk., 2M, 30 Apr 1983, R. M. Shelley and P. B. Nader (NCSM A4079).

FLORIDA: *Walton Co.,* Gaskin, F, 29 Feb 1960, R. Cordle (FSCA); DeFuniak Springs, M, 6F, 7 Oct 1958, collector unknown (FSCA); and 8.5 mi. W DeFuniak Springs, along US hwy. 90, 7M, 2F, 22 Jan 1965, N. B. Causey (FSCA). *Washington Co.,* Chipley, 2M, F, 23 Jan 1965, N. B. Causey (FSCA). *Bay Co.,* Panama City, M, 2 Feb 1960, R. E. Woodruff (FSCA) and 2M, 5 Mar 1961, R. C. Hallman (FSCA). *Jackson Co.,* Florida Caverns St. Pk., M, 3F, 27 May 1968, R. E. Woodruff, and M, 2F, 14 Apr 1960, H. V. Weems (FSCA); Marianna vic., M, 26 Mar 1961, L. Hubricht (RLH) and M, 3 Apr 1968, J. A. Beatty (WAS); Cottondale, M, 31 Jul 1960, L. Hubricht (RLH); Three Rivers St. Pk. and Sneads vic., M, 2F, 7 Sep 1959, and 2M, 2 Mar 1961, L. Hubricht (RLH), M, 15 May 1964, M. Muma (FSCA), and 2M, F, 19 Jul 1973, W. A. Shear (WAS). *Calhoun Co.,* 2 mi. NW Chason, F, 4 Feb 1960, T. E. Kunkle (FSCA). *Liberty Co.,* along Appalachicola R. nr. Bristol, M, F, 24 Jan 1965, N. B. Causey (FSCA) and Torreya St. Pk., M, 15 Mar 1963, H. W. Levi (MCZ), and 5M, 3F, 24 Jan 1965, N. B. Causey, and M, 22 Apr 1967, P. C. Drummond (FSCA). *Leon Co.,* Tallahassee, many MM and FF collected from 1953-1959 by H. A. Denmark, H. V. Weems, and others (FSCA); Tall Timbers Res. Sta, ca. 22 mi. N Tallahassee, M, 2F, 5 Aug

1958, W. W. Baker (FSCA) and M, 30 Jul 1973, D. Harris (FSCA). *Jefferson Co.,* Monticello, M, 4F, 29 Aug 1959, H. W. Collins (FSCA); and Big Bend Horticultural Lab., 8M, date and collector unknown (FSCA) and 2M, 1971, H. Whitcomb (FSCA). *Hamilton Co.,* Suwannee River St. Pk., White Springs, 2F, 29 May 1958, N. B. Causey (FSCA).

*Dicellarius bimaculatus lamellidens* (Chamberlin), new status
Figs. 7–8

*Fontaria lamellidens* Chamberlin, 1931:78–79.—Attems, 1938:167.
*Spathoria lamellidens.*—Chamberlin, 1939:6, pl. 1, fig. 9.
*Dicellarius lamellidens.*—Chamberlin and Hoffman, 1958:30.

*Type specimen.*—The male holotype is missing from the RVC collection where Chamberlin (1931) and Chamberlin and Hoffman (1958) report its deposition. The type locality is Biloxi, Harrison Co., Mississippi, and since there are no paratypes, the following diagnosis is prepared from males from Ocean Springs in adjacent Jackson County.

*Diagnosis.*—Gonopods in situ with acropodites bent strongly mediad, crossing at about ¾ length and extending beyond each other; prefemoral process short, terminating below level of acropodite division, moderately wide basally and tapering to acuminate tip, directed across acropodite stem; acropodite in medial view curved subcaudad, solenomerite overlying tibial process, latter longer and wider than solenomerite, profile visible.

*Variation.*—The degree of caudal curvature of the acropodite, as seen in medial view, varies and is stronger in the Stone County males.

*Distribution.*—Known only from a small area in coastal Mississippi west of the Pascagoula River. It has not been taken west of Long Beach, a suburb of Gulfport-Biloxi, but it could conceivably extend to the Pearl River and possibly even into southeastern Louisiana. Specimens were examined as follows:

MISSISSIPPI: *Stone Co.,* between Harrison Co. line and MS hwy. 26, 3M, 21 Jan 1965, N. B. Causey (FSCA). *Jackson Co.,* Ocean Springs, Gulf Hills, 3M, 2F, 2 Oct 1958, and 3M, 1 Jun 1961, N. B. Causey (FSCA); and Gulf Coast Research Lab. nr. Ocean Springs, M, 16 Mar 1957, D. Moore; 2M, F, 1 Oct 1958, collector unknown; M, F, 30 May 1959, N. B. Causey; 2M, F, 27 November 1964, C. Guise; and M, 21 Nov 1965, D. E. Hahn (all FSCA). *Harrison Co.,* Long Beach, F, 20 Mar 1910, collector unknown (RVC).

*Remarks.*—In medial view the acropodite of *D. b. lamellidens* curves in the opposite direction to that of *D. b. fictus* (compare Figs. 6 and 8). However, the two forms connect through a series of intermediate stages along the Gulf Coast and therefore represent geographic races of a single species rather than different species.

*Dicellarius bimaculatus* intergrades

Intergrade populations of *D. bimaculatus* occur east of the Pascagoula River in Jackson County, Mississippi. The acropodites curve less than those from Ocean Springs (Fig. 8) and the gap between the distal elements is slightly visible in medial view. This configuration is intermediate between the nominate subspecies and *D. b. lamellidens.* Specimens were examined as follows:

MISSISSIPPI: *Jackson Co.*, Pascagoula, M, Sep 1953, E. Waitt (FSCA) and 3M, F, 1 Jan 1954, N. B. Causey (FSCA); and Spanish Fort, 2M, 4F, 15 Jun 1953, collector unknown (FSCA) and 2M, F, 21 Jan 1965, N. B. Causey (FSCA).

*Dicellarius okefenokensis* (Chamberlin)
Figs. 9–12

*Leptodesmus okefenokensis* Chamberlin, 1918:370–371.
*Dicellarius okefenokensis.*—Chamberlin, 1920:97.—Chamberlin and Hoffman, 1958:31.
*Epeloria nannoides* Chamberlin, 1949:101, fig. 24.

*Type specimens.*—Male holotype (MCZ) taken by unknown collector, Dec 1913, on Billy's Island in the Okefenokee Swamp, Charlton Co., Georgia.

*Diagnosis.*—Prefemoral process not extending across stem of acropodite; latter bent broadly anteriad at midlength, overhanging and extending slightly beyond level of prefemoral process, with torsion, prostatic groove crossing from medial to lateral sides at anterior bend; tibial process overlying and masking most of solenomerite in medial view.

*Holotype.*—Length 22.0 mm, maximum width 4.2 mm, W/L ratio 19.1%, depth/width ratio 73.8%. Segmental widths as follows:

| | | | |
|---|---|---|---|
| collum | 3.4 mm | 11th–16th | 4.0 |
| 2nd | 3.6 | 17th | 3.6 |
| 3rd | 3.9 | 18th | 2.9 |
| 4th–10th | 4.2 | | |

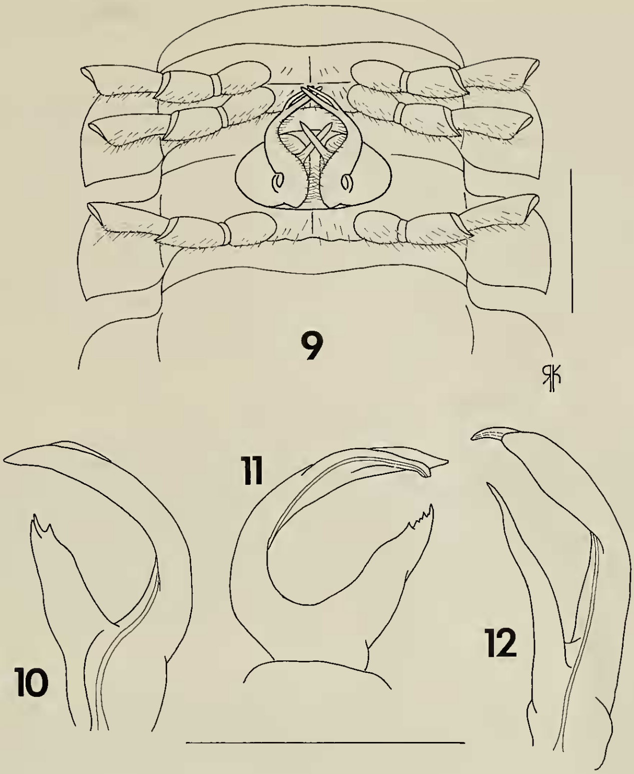
Color in life unknown.

Somatic features similar to those of *D. b. bimaculatus* with following exceptions: Width across genal apices 2.4 mm, interantennal isthmus 0.9 mm. Antennae reaching back nearly to caudal edge of 4th segment, relative lengths of antennomeres $2 > 6 > 5 > 4 = 3 > 1 > 7$. Genae with very slight medial impression. Facial setae as follows: Epicranial 3-3, interantennal 1-1, frontal 1-1, genal 3-3, clypeal about 12-12, larbral about 16-16.

Collum moderately broad, ends extending slightly beyond those of following tergite. Peritremata extremely thick and conspicuous, enlarged caudad.

Sternum of segment 5 with 2 moderately elevated areas between 4th legs and slight recession between 5th legs, 6th sternum with convex recession between both leg pairs, 7th legs set slightly farther apart than 6th. Postgonopodal sterna with slight midline elevation on segments 11–17, elevation oriented transversely rather than longitudinally as in other species.

Gonopodal aperture elliptical, 1.6 mm wide and 0.5 mm long at midpoint, indented anteriolaterally, sides flush with metazonal surface. Gonopods in situ (Fig. 9, not this specimen) with acropodites curving broadly mediad at midlength and extending beyond anterior margin of aperture, apices overlapping above 6th sternum; prefemoral processes directed anteriomediad, crossing at midlength in midline of aperture, apices extending slightly beyond anterior margin of aperture. Gonopod structure as follows (Figs. 10–11): Prefemoral process wide and long,




Figs. 9–12. *Dicellarius okefenokensis*: 9, Gonopods in situ, ventral view of male from Columbia Co., FL; 10, Telopodite of left gonopod of holotype, medial view; 11, The same, lateral view; 12, Telopodite of left gonopod of male from Hernando Co., FL, medial view. Scale line for Fig. 9 = 1.00 mm; line for other Figs. = 1.00 mm for each.

about ⅔ length of acropodite, spatulate basally with sinuous margins narrowing at midlength, apex with several minute teeth directed toward tip of acropodite. Acropodite in form of broadly curved arc with torsion, overhanging and extending slightly beyond level of prefemoral process, prostatic groove crossing to lateral surface proximad, distal division masked in medial and lateral views, located at about ⅔ length. Distal elements widely separated, diverging continuously with greatest separation apically, gap visible mostly in ventral or dorsal perspectives; solenomerite anterior to, and slightly shorter than, tibial process, sides narrowing smoothly to tip; tibial process overlying and largely obscuring solenomerite in medial view, broader than latter, sides parallel for most of length, apically acute. Prostatic groove arising in pit in prefemur, running along medial surface of acropodite basally, crossing to lateral side at anterior bend, terminating apically on solenomerite.

*Description of females.*—Since the type collection contains no females and none have been encountered in Georgia, the following description has been prepared from females from Baker County, Florida, the closest available to the type locality. Length 23.2 mm, maximum width 4.0 mm, W/L ratio 17.2%, depth/width ratio 72.5%. Agreeing essentially with males in somatic features except paranota more strongly depressed, creating appearance of more highly arched body, and sternal elevations greatly reduced barely visible.

Cyphopods in situ with opening of valves visible in aperture. Receptacle absent. Valves relatively large, subequal, surface finely granulate. Operculum relatively large, located under dorsolateral corner of valves, surface finely granulate.

*Variation.*—Southern populations vary considerably from those north of Gainesville. The prefemoral process is longer but of the same length relative to the acropodite since the latter is also longer; its width also varies, as it becomes much narrower and more acicular with decreasing latitude. The acropodite bends more abruptly at midlength (Fig. 12), and the solenomerite is longer relative to the tibial process, projecting beyond the latter in medial view.

*Ecology.*—According to the labels in the vials, *D. okefenokensis* is typically found under logs in moist, predominantly hardwood habitats. The sample from Waycross, Georgia, was discovered under trash in a yard.

*Distribution.*—Southeastern Georgia and peninsular Florida nearly to the level of Tampa. Except for the Waycross sample, all specimens have come from south of the Suwannee River or its headwaters in the Okefenokee Swamp. The known Florida localities all lie north of highway I-4. Specimens were examined as follows:

GEORGIA: *Ware Co.,* Waycross, under trash in yard, 2M, 8 Feb 1962, M. Barnette (FSCA). *Charlton Co.,* Billy's Island, Okefenokee Swamp, M, Dec 1913, collector unknown (MCZ) TYPE LOCALITY.

FLORIDA: *Nassau Co.,* Austin Cary Forest, M, 30 Jun 1960, W. J. Platt (FSCA). *Baker Co.,* Macclenny, M, 26 Dec 1960, E. W. Holder (FSCA); and Glen St. Mary, 2M, 3F, 18 Jan 1961, E. W. Holder (FSCA). *Columbia Co.,* Osceola Nat. For., 6M, 15 Feb and 16 Mar 1977, J. R. Wiley (FSCA). *Hamilton Co.,* White Springs, M, F, 1959, A. Williams (FSCA). *Suwannee Co.,* along Rocky Cr. at rd. S-136, M, F, 16 Mar 1977, J. R. Wiley (FSCA). *Clay Co.,* no further locality, 2F, 7 Jan 1961, H. A. Denmark (FSCA). *Marion Co.,* Confederate Cave, M, 19 Feb 1959, R. Cumming (FSCA). *Alachua Co.,* 1 mi. N Newberry, along US hwy. 27, F, 14 Jan 1967, J. E. Lloyd (FSCA); and Gainesville, many MM and FF collected mostly during Oct–Feb from 1933–1965, by about 10 collectors (RVC, MCZ, RLH, & FSCA). *Putnam Co.,* Ocala Nat. For., Johnson Field, F, 21 Jan 1973, R. Skinner (AU). *Seminole Co.,* Sanford, M, 14 Feb 1960, G. W. Desin (FSCA). *Hernando Co.,* Brooksville, M, 25 Jan 1960, L. Hill (FSCA); and 10 mi. S Floral City, along US hwy. 41, 2M, 23 Dec 1973, W. A. Shear (RLH). *Pasco Co.,* Dade City, M, 15 Feb 1972, K. C. Lowery (FSCA), and M, 14 Jun 1983, R. M. Shelley and J. L. Staton (NCSM A4160).

*Remarks.*—*Dicellarius okefenokensis* is the only allopatric species in the genus. Its range does not overlap that of any other species, though it abuts *D. b. fictus* in the west.

The acropodite of *D. okefenokensis* is unique to both the genus and tribe in displaying two features typically found and convergent in the tribe Apheloriini: the broadly curved acropodite that overhangs the prefemoral process in medial view, and torsion, which causes the prostatic groove to cross from medial to lateral sides at ⅓ length. Just as the acropodite in *D. b. lamellidens* is turned counterclockwise so that the solenomerite overlies the tibiotarsus in medial view, the acropodite of *D. okefenokensis* probably evolved from eastern populations of *D. bimaculatus* in which the reverse, or clockwise, twisting occurred. Such rotation would place the tibiotarsus over the solenomerite in medial view, and an early stage in this torsion is apparent in some males of *D. b. fictus,* where the edge rather than the side of the solenomerite is visible medially. Thus, I think *D. okefenokensis* represents an eastern population of *D. bimaculatus* in which the distal half of the acropodite has turned about 90° clockwise, just as *D. b. lamellidens* represents ones in which 90° counterclockwise rotation has occurred. The latter still links with other populations of *D. bimaculatus* by intermediate or intergrade forms, and consequently is only a geographic race. Connections between *D. okefenokensis* and *D. bimaculatus* have disappeared, however, and the former has achieved reproductive isolation as evidenced by the torsion, the broadened curvature of the acropodite, and reduced body size.

### *Dicellarius talapoosa* (Chamberlin)

*Diagnosis.*—Acropodite with slight but continuous curve; distal elements narrowly separated or touching, continuing general curvature of acropodite, never overlying one another in medial or lateral views; solenomerite acicular, with sides tapering smoothly and continuously to subacuminate tip; tibial process acicular, shorter than solenomerite; prefemoral process angling across stem of acropodite, relatively short, extending at most to base of distal elements, tip overlying tibial process.

*Remarks.*—*Dicellarius talapoosa* occurs inland from *D. bimaculatus* in Alabama and Georgia. Its range abuts that of *D. b. fictus* in the south, and it is sympatric in parts of the range with both *D. atlanta* and *D. sternolobus.* In the material available to me a consistent difference exists in the degree of separation of the distal elements in populations east and west of the Coosa River. In the eastern populations they are contiguous for most of their lengths, whereas in the western ones they are narrowly, but completely, separated. One sample from St. Clair County, an intermediate geographical position, displays an intermediate degree of separation that I consider an intergrade. This situation is a much clearer indication of geographic races than that of *D. bimaculatus,* and since Chamberlin's type is the eastern form, it becomes the nominate subspecies and a new subspecific name is needed for the western form. I hereby propose *D. t. separandus* to signify the greater separation of the solenomerite and tibial process.

### *Dicellarius talapoosa talapoosa* (Chamberlin), new combination, new status
Figs. 13–14

*Epeloria talapoosa* Chamberlin, 1939:3, pl. 1, fig. 1.—Chamberlin and Hoffman, 1958:33.

*Type specimens.*—Male holotype and one male paratype (RVC) collected by R. V. Chamberlin, 29 Jul 1910, from Tallapoosa, Haralson Co., Georgia. Chamberlin (1939) reported that a female allotype was taken in addition to the holotype, which is what the sample label says, but the vial actually contains two males, one of which must be a paratype.

*Diagnosis.*—Distal elements closely appressed together, touching for most of length except for slight basal gap.

*Holotype.*—Body badly fragmented and unmeasurable, segmental widths taken from male from Cleburne Co., Alabama, the closest whole specimen to the type locality, and listed under variation.

Color in life unknown.

Somatic features similar to those of *D. b. bimaculatus,* with following exceptions:

Width across genal apices 4.4 mm. Antennae extending to caudal edge of 3rd tergite, relative lengths of antennomeres 6 > 5 > 3 = 4 = 2 > 1 > 7. Facial setae as in *D. b. bimaculatus* except subantennal 1-1, genal 2-2, and clypeal about 12-12.

Collum moderately broad, ends extending well beyond those of following tergite.

Fourth sternum without process; 5th sternum with two elevated, medially coalesced flattened areas between 6th legs and deep convex recession between 7th legs. Postgonopodal sterna with midline elevations in form of narrow, longitudinal ridges, distinct on segments 10–15.

Gonopodal aperture 2.4 mm wide and 0.8 mm long at midpoint, indented slightly anteriolaterally, sides flush with metazonal surface. Gonopods in situ (Fig. 13, not this specimen) with acropodites projecting anteriad from aperture, extending well beyond anterior margin of aperture, with apices crossing between 7th legs, prefemoral processes also overlapping and extending beyond aperture. Gonopod structure as follows (Fig. 14): Prefemur moderate in size, with relatively short, acicular prefemoral process extending in medial view across stem of acropodite approximately half the length of the latter, terminating near level of distal division of latter. Acropodite curving slightly caudad, sides narrowing gradually and divided at about ⅔ length into distal elements; latter subspiniform and apically acute, closely appressed together, touching for most of length, with slight basal separation visible in subanterior view; solenomerite slightly longer and more acute. Prostatic groove arising in pit in prefemur, running along medial side of acropodite stem to level of distal elements, curving toward anterior margin of acropodite and entering solenomerite, opening apically.

*Male paratype.*—The male paratype agrees with the holotype in all particulars and is also fragmented and unmeasurable.

*Description of Females.*—Since the type collection contains no females, the following description was prepared from specimens from Randolph County, Alabama, the closest females available to the type locality. Length 42.1 mm, maximum width 8.8 mm, W/L ratio 20.9%, depth/width ratio 72.7%. Agreeing essentially with holotype in most somatic feature, except paranota more strongly depressed, giving appearance of more highly arched body, and sternal elevations greatly reduced, barely detectable.

Cyphopods in situ with valvular openings visible in aperture; valves large, subequal, surface finely granulate. Receptacle absent. Operculum small, located on lateral side of valves, surface finely granulate.

*Variation.*—The sample from Cheaha State Park, Cleburne Co., Alabama (NCSM

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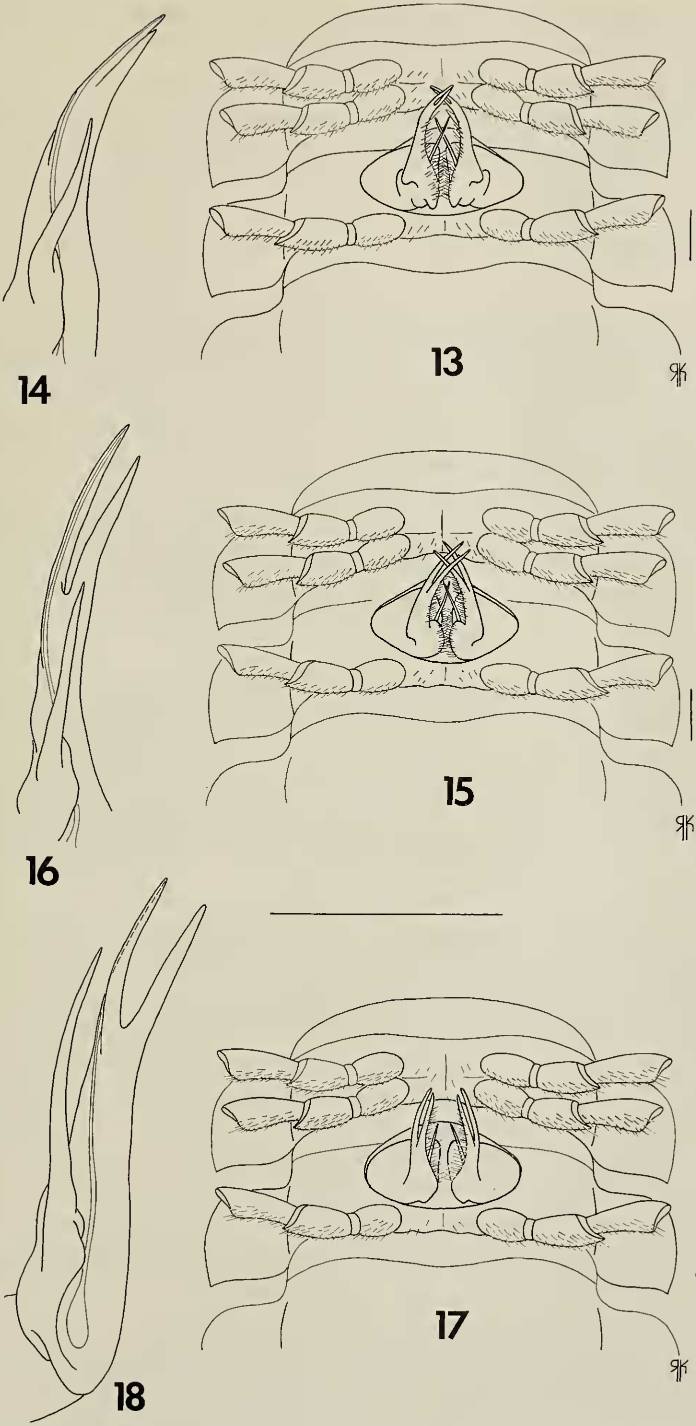
Figs. 13–16. *Dicellarius talapoosa*: 13–14, *D. t. talapoosa.* 13, Gonopods in situ, ventral view of male from Cleburne Co., AL; 14, Telopodite of left gonopod of holotype, medial view; 15–16, *D. t. separandus.* 15, Gonopods in situ, ventral view of paratype; 16, Telopodite of left gonopod of holotype,




medial view. Figs. 17–18, *Dicellarius atlanta*: 17, Gonopods in situ, ventral view of male from Peach Co., GA; 18, Telopodite of left gonopod of holotype, medial view. Scale lines for Figs. 13, 15, and 17 = 1.00 mm; line for other figs. = 1.00 for Fig. 14, 1.14 mm for 16, and 0.80 mm for 18.

A3117), is the closest to the type locality with whole males, one of whose measurements are as follows: Length 34.8 mm, maximum width 7.7 mm, W/L ratio 22.1%, depth/width ratio 66.2%. Segmental widths as follows:

| | | | |
|---|---|---|---|
| collum | 5.8 mm | 6th–13th | 7.7 |
| 2nd | 6.3 | 14th | 6.8 |
| 3rd | 7.1 | 15th | 6.6 |
| 4th–5th | 7.3 | 16th | 6.3 |
| | | 17th | 5.8 |
| | | 18th | 5.1 |

The gonopods of this subspecies are quite uniform. The prefemoral processes tend to be longer and the acropodites more distinctly curved in western populations. However, the distal elements are always closely appressed together, except for the slight gap at their bases, and their lengths relative to each other and to the overall acropodite do not change.

*Distribution.*—The range of *D. t. talapoosa* lies in the Piedmont Plateau and Fall Zone of west-central Georgia and east-central Alabama, east of the Coosa River. It crosses the Coosa River in the north and extends onto Lookout Mountain along the northern Alabama-Georgia boundary. Specimens were examined as follows:

GEORGIA: *Dekalb Co.,* Oglethorpe Univ., M, date unknown, A. L. Cain (FSCA). *Haralson Co.,* Tallapoosa, 2M, 29 Jul 1910, R. V. Chamberllin (RVC) TYPE LOCALITY; and Bremen, M, 29 Jul 1910, R. V. Chamberlin (RVC).

ALABAMA: *Dekalb Co.,* 4.4 mi. SE Mentone, along AL hwy. 117 at Anna Branch Cr., M, F. 15 Apr 1978, R. M. Shelley and R. E. Ashton (NCSM A18442). *Etowah Co.,* 1.5 mi. W Hokes Bluff, along Coosa R., 2M, 28 Feb 1961, L. Hubricht (RLH). *Cleburne Co.,* 3.4 mi. N Shoal Cr. Camping Area, M, 28 Oct 1960, L. Hubricht (RLH); 4 mi. W Heflin, M, 5 Mar 1961, L. Hubricht (RLH); and summit Cheaha Mtn., Cheaha St. Pk., M, 10 Jun 1953, L. Hubricht (RLH) and 13 M, F, 20 May 1980, R. M. Shelley (NCSM A3117). *Talladega Co.,* 5 mi. W Sylacauga, M, 3 Mar 1973, W. Redmond (AU). *Lee Co.,* 3 mi. N Auburn, along AL hwy. 143 at Saugahatchee Cr., M, 7 Mar 1973, T. French (AU). *Randolph Co.,* 0.7 mi. W Wadley, F, 1 Oct 1960, L. Hubricht (RLH). *Macon Co.,* Tuskegee Nat. For., M, 2F, 14 May 1973, R. B. Little (AU); and Tuskegee, Tuskegee Institute Campus, 2M, 14 Mar 1978, S. B. Ruth (NCSM A3891).

*Remarks.*—I collected 13 males on the roadway near the summit of Cheaha Mountain early in the morning of 20 May 1980. The animals must have ventured forth in the cool weather of the preceding night, and six had been freshly decapitated by an unknown predator. The head and first three to four segments had been removed, but the bite stopped short of segment 5 and the anteriormost defensive glands. I have seen this phenomenon twice before, with individuals of *Croatania catawba* Shelley from Chester Co., South Carolina, and *Gyalostethus monticolens* (Chamberlin) from the Great Smoky Mountains National Park, Swain Co., North Carolina. In all instances the segments seem to have been removed by a single, clean bite, as there is no evidence of continuous chewing. At Cheaha Mountain the millipeds were exposed on the pavement away from protective cover, but in the other sites they were in forests lying on top of the litter.

*Dicellarius talapoosa separandus,* new subspecies
Figs. 15–16

*Type specimens.*—Male holotype (NCSM A3132) and 4 male and 4 female paratypes collected by R. M. Shelley, 23 May 1980, at Rickwood Caverns State Park, Blount Co., Alabama. Male and female paratypes deposited in FSCA.

*Diagnosis.*—Distal elements subparallel but not touching, separated for entire lengths, diverging apically.

*Variation.*—The degree of separation of the distal elements varies, but otherwise all males are closely similar to the holotype.

*Distribution.*—This subspecies occurs generally west of the Coosa River, in the Cumberland Mountains around Birmingham and the Appalachian Plateau. It is sympatric and syntopic with *T. lampra* in Tuscaloosa. Specimens were examined as follows:

ALABAMA: *Dekalb Co.,* 3.7 mi. NW Collinsville, along AL hwy. 68 at Little Cr., 2.5 mi. W jct. I-59, M, 15 Apr 1978, R. M. Shelley and R. E. Ashton (NCSM A1841). *Morgan Co.,* 8 mi. S Decatur, along Flint Cr., M, 24 May 1980, R. M. Shelley (NCSM A3143). *Blount Co.,* Rickwood Caverns St. Pk., 5M, 4F, 23 May 1980, R. M. Shelley (NCSM A3132) TYPE LOCALITY. *Jefferson Co.,* Birmingham, 3M, 16–25 Nov 1958, collector unknown (FSCA). *Tuscaloosa Co.,* Tuscaloosa, M, 2 juvs., 29 Mar 1948, G. Ball (RLH).

*Remarks.*—The in situ gonopodal configuration of this subspecies is the same as that of the nominate, except the wider gap between the distal elements allows them to crisscross (Fig. 15, of paratype). The acropodites simply overly each other in *D. t. talapoosa* (Fig. 13).

The sample from Birmingham had the following note about the smell of the defensive secretion: "odor good, strong, pineapple, with dash of shoe polish; not too unpleasant, sweetish."

*Dicellarius talapoosa* intergrades

In two males from St. Clair County, the basal gap between the distal elements is larger than in *D. t. talapoosa,* but they still touch distally. I regard these specimens as intergrades, and they are indicated by the northernmost "X" in Fig. 29. They were taken about 5 miles west of the Coosa River, which generally forms the boundary between the subspecies. The data are as follows:

ALABAMA: *St. Clair Co.,* Steele, 2M, 4 Apr 1948, H. E. Evans (RLH).

*Dicellarius atlanta* (Chamberlin), new combination
Figs. 17–18

*Epeloria atlanta* Chamberlin, 1946b:151–152, fig. 7.—Chamberlin and Hoffman, 1958:32.

*Type specimens.*—Male holotype and female allotype (RVC) collected by P. W. Fattig, 1 Dec 1945, from Atlanta, Georgia. The label in the vial states 1946, but this must be incorrect since it would not have allowed publication in that year. Neither the publication nor the label in the vial gives the county, but since Atlanta was much smaller in the 1940's and its center is in Fulton Co., the type specimens were probably collected there rather than in Dekalb Co.

*Diagnosis.*—Acropodite relatively straight, sublinear; distal elements widely separated, either continuous with sublinear acropodite or very slightly curved, never overlying one another in medial or lateral views; solenomerite acicular, sides tapering smoothly and continuously to subacuminate tip; tibial process acicular, subequal in length to solenomerite; prefemoral process straight, not angling across acropodite stem but lying over or near anterior margin, relatively long, extending well beyond base of distal elements with tip either over solenomerite or on anterior side of latter.

*Holotype.*—Length 30.3 mm, maximum width 6.0 mm, W/L ratio 19.8%, depth/width ratio 66.4%. Segmental widths as follows:

| | | | |
|---|---|---|---|
| collum | 5.0 mm | 16th | 5.8 |
| 2nd–4th | 5.5 | 17th | 5.5 |
| 5th | 5.8 | 18th | 4.6 |
| 6th–15th | 6.0 | | |

Color in life unknown.

Somatic features similar to those of *D. b. bimaculatus,* with following exceptions:

Width across genal apices 4.1 mm, interantennal isthmus 1.3 mm. Antennae extending back to caudal edge of 3rd tergite, relative lengths of antennomeres $6 > 5 > 4 = 3 = 2 > 1 > 7$. Genae with distinct, linear, diagonal impression. Facial setae as in *D. b. bimaculatus* except genal 2-2, clypeal about 11-11, labral about 18-18.

Collum moderately broad, ends extending slightly beyond those of following tergite.

Sternum of segment 5 with small elevated area between 4th legs and depression between 5th legs; 6th sternum with wide, flattened, elevated area between 6th legs and deep, convex recession between 7th legs. Postgonopodal sterna with midline elevations generally large and distinct, acute and subconical, largest on segments 11–14, lower and more rounded before and after.

Gonopodal aperture ovoid, 2.4 mm wide and 1.0 mm long at midpoint, indented anteriolaterad, sides nearly flush with segmental surface. Gonopods in situ (Fig. 17, not this specimen) with acropodites projecting anteriad from aperture, subparallel, not overlapping or crossing, extending beyond anterior margin of aperture to between 7th legs. Gonopod structure as follows (Fig. 18): Prefemur moderate, with long, acicular prefemoral process extending well beyond level of distal division of acropodite on anterior side. Acropodite extending sublinearly from prefemur, bent slightly caudad at level of division, sides parallel, not tapering, divided roughly at ⅔ length. Distal elements well separated, diverging apically; tibial process apically blunt; solenomerite slightly longer, tapering distad to subacuminate tip. Prostatic groove arising in pit in prefemur, running along medial surface of acropodite to level of division, crossing to anterior side and opening terminally on solenomerite.

*Female allotype.*—Length 31.3 mm, maximum width 5.4 mm, W/L ratio 17.4%, depth/width ratio 77.8%. Agreeing closely with male except paranota more strongly depressed, creating appearance of more highly arched body, and sternal elevations greatly reduced, barely detectable.

Cyphopods in situ with openings of valves visible in aperture; valves large, subequal, surface finely granuate. Receptacle absent. Operculum relatively large, located under lateral end of valves, surface finely granulate.

*Variation.*—The gonopods of *D. atlanta* are uniform. The acropodite always extends linearly from the prefemur, and the solenomerite is always slightly longer than the tibial process. The distal elements continue in the axis of the acropodite stem, although they lean slightly caudad in some males; they converge apically in specimens from Paulding County, and the solenomerite is bowed outward basally away from the tibiotarsus. In medial view the prefemoral processes lean anteriad basally away from the acropodite then curve back toward the latter at midlength.

*Distribution.*—*Dicellarius atlanta* is the only species occurring in the southern Blue Ridge Province (Appalachian Mountains) and ranges from western North Carolina to central Georgia and eastern Alabama. Its range overlaps those of *D. b. fictus* and *D. t. talapoosa* in central Georgia, and it is sympatric and syntopic with *T. bifida* in Dawson and Houston Counties, Georgia. The range spans the Chattahoochee River and the headwaters of the Ocmulgee River, and may also traverse the Savannah River into Oconee County, South Carolina.

NORTH CAROLINA: *Graham Co.,* 2 mi. NW Milltown, nr. Snowbird Picnic Area, 2M, 10 May 1961, L. Hubricht (RLH).

GEORGIA: *Rabun Co.,* Tallulah Falls, M, 28 Apr 1943, W. Ivie (RVC). *Habersham Co.,* Clarkesville, F, 4 Apr 1943, collector unknown (RVC). *Dawson Co.,* Amicalola Falls St. Pk., 2M, 2F, 16 Apr 1978, R. M. Shelley and R. E. Ashton (NCSM A1855). *Jackson Co.,* NW of Pendergrass, M, 23 Apr 1943, W. Ivie (RVC). *Clarke Co.,* Athens, Univ. of GA campus, F, 27 Feb 1944, E. P. Odum (RVC); and 9 mi. W Athens, M, 6 May 1961, L. Hubricht (RLH). *Oconee Co.,* Watkinsville, M, 26 Mar 1959, M. Pitken (FSCA). *Fulton Co.,* Atlanta, M, F, 1 Dec 1946, P. W. Fattig (RVC), and Ft. McPherson, 2F, 9 Dec 1943, D. E. Beck (RVC). *Dekalb Co.,* Atlanta, 2M, 2F, 7 Oct 1960, E. Davidson (FSCA); and Stone Mountain, M, F, 20 Oct 1946, and M, 6 Apr 1947, P. W. Fattig (RVC). *Douglas Co.,* Sweetwater Creek St. Pk., M, 21 Nov 1977, R. M. Shelley (NCSM A1796). *Paulding Co.,* Dallas, M, 30 Mar 1947, P. W. Fattig (RVC). *Clayton Co.,* 6.4 mi. S Corely, M, 4 Dec 1960, L. Hubricht (RLH). *Butts Co.,* Indian Springs St. Pk., M, 4F, 20 Nov 1977, R. M. Shelley (NCSM A1789). *Bibb Co.,* Macon, M, 4 Mar 1961, L. Hubricht (RLH). *Peach Co.,* 2 mi. W Fort Valley, along GA hwy. 96, 4M, F, 12 Apr 1978, R. M. Shelley (NCSM A1834). *Houston Co.,* Perry, 50M, 9F, 26–28 Dec 1982, J. A. Payne (RLH). *Meriwether Co.,* 3.5 mi. S Woodbury, M, 11 Mar 1961, L. Hubricht (RLH). *Harris Co.,* Franklin D. Roosevelt St. Pk., M, 2 May 1983, R. M. Shelley and P. B. Nader (NCSM A4083). *Muscogee Co.,* Columbus College, M, 2 Nov 1977, G. E. Stanton (CC).

ALABAMA: *Lee Co.,* Auburn, M, Mar 1966, H. B. Cunningham (AU); Prather's Pond nr. Auburn, 8M, 2F, Mar 1973, T. French (AU); and 3 mi. N Auburn, along AL hwy. 143 at Saugahatchee Cr., 3M, Apr 1973, T. French (AU).

*Remarks.*—As shown in Figs 16 and 18, the gonopod of *D. atlanta* is closely similar to that of *D. t. separandus,* the main differences being the orientation of the prefemoral process, the degree of separation of the distal elements, and the curvature of the acropodite. In *D. t. separandus* the prefemoral process angles across the stem of the acropodite, whereas in *D. atlanta* it is located entirely on the anterior side. The distal elements are subequal and more widely separated in *D. atlanta,* and the acropodite is more linear in this species. These similarities suggest that *D. atlanta* originated as a subspecies of *D. talapoosa,* and has since achieved reproductive isolation as evidenced by the range overlap with *D. t. talapoosa.*

*Dicellarius sternolobus* Loomis
Figs. 19–23

*Dicellarius sternolobus* Loomis, 1969:247–248, figs. 5–7.

*Type-specimen.*—Male holotype (NMNH) taken by unknown collector, 27 Oct 1944, from Alexander City, Tallapoosa Co., Alabama. The fragmented, immature paratype in the FSCA does not appear to be this species.

*Diagnosis.*—Sterna of segments 4 and 5 with large, ventrally directed processes, usually longer than widths of adjacent coxae; solenomerite overlying tibial process in medial view, much narrower than latter with sides tapering smoothly and continuously to subacuminate tip; lateral surface of tibial process irregular, with several grooves and ridges.

*Holotype.*—Length 36.8 mm, maximum width 6.8 mm, W/L ratio 18.5%, depth/width ratio 75.0%. Segmental widths as follows:

| | | | |
|---|---|---|---|
| collum | 5.4 mm | 7th–15th | 6.8 |
| 2nd | 6.0 | 16th | 6.5 |
| 3rd–5th | 6.2 | 17th | 5.9 |
| 6th | 6.6 | 18th | 5.4 |

Color in life unknown.

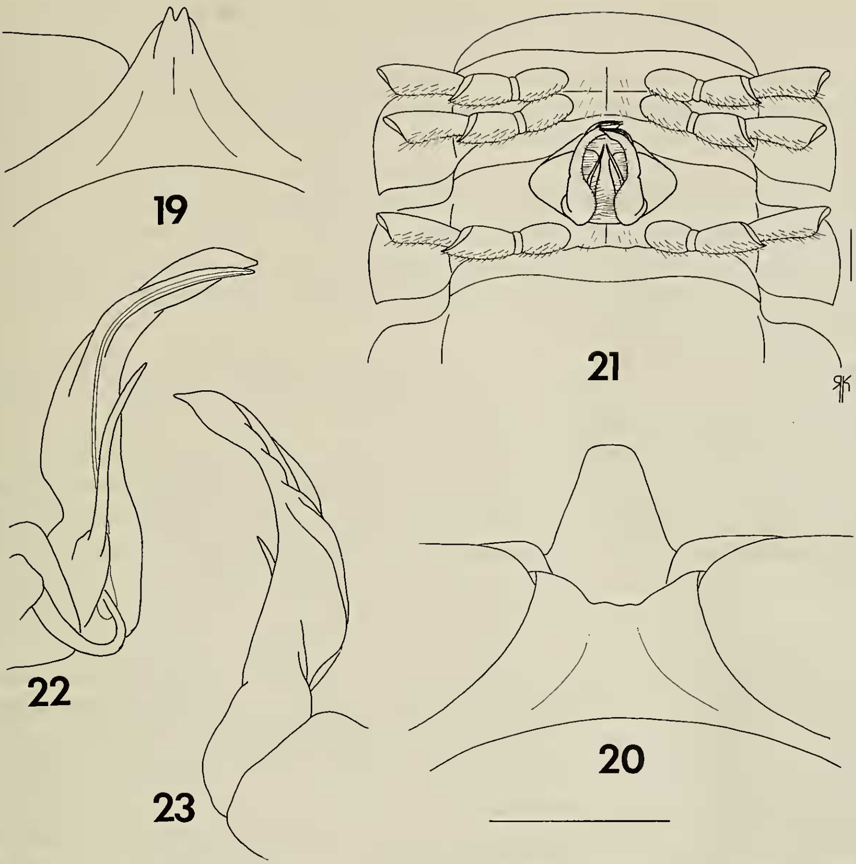
Somatic features similar to those of *D. b. bimaculatus,* with following exceptions:

Width across genal apices 4.5 mm, interantennal isthmus 1.2 mm. Antennae reaching back to middle of 4th tergite, relative length of antennomeres $2 > 3 > 6 = 5 = 4 > 1 > 7$. Genae with distinct medial depression. Facial setae as in *D. b. bimaculatus* except subantennal 1-1, genal 2-2, clypeal about 14-14, labral about 20-20.

Collum broad, ends extending slightly beyond those of following tergite. Dorsum smooth and polished, glossy.

Sternum of segment 4 with large, apically divided process between 3rd legs, greater in length than widths of adjacent coxae (Fig. 19); 5th sternum with similar process between 4th legs, longer than widths of adjacent coxae, and with slight recession between 5th legs (Fig. 20); 6th sternum with two low, transverse ridges between 6th legs and depression between 7th, 7th legs set slightly farther apart than 6th. Postgonopodal sterna with lowly rounded, faint midline elevations noticeable on segments 8–13, undetectable on remaining segments.

Gonopodal aperture ovoid, 2.1 mm wide and 1.0 mm long at midpoint, indented anteriolaterad, sites flush with metazonal surface. Gonopods in situ (Fig. 21, not this specimen) with acropodites bending mediad distad, apices overlapping; prefemoral processes angling mediad but not touching. Gonopod structure




Figs. 19–23. *Dicellarius sternolobus*: 19, Sternum of segment 4 of holotype, caudal view; 20, Sternum of segment 5 of the same, caudal view; 21, Gonopods in situ, ventral view of male from Shelby Co., AL; 22, Left gonopod of holotype, medial view; 23, Telopodite of the same, lateral view. Scale line for Fig. 21 = 1.00 mm; line for other Figs. = 0.81 mm for Fig. 19, 1.00 mm for Figs. 20 and 22–23.

as follows (Fig. 22–23): Prefemoral process acicular, curved slightly at midlength and angling across stem of acropodite to level of distal division. Acropodite curved gently caudad at midlength, overhanging and extending well beyond level of prefemoral process; stem widening basally then narrowing gradually to level of division at ⅓ length. Distal elements subparallel and subequal in length, narrowly separated, gap obscured in medial and lateral views but visible from dorsal and ventral perspectives; solenomerite located medial to tibial process and overlying it in this perspective, narrow and acicular, continuing general curvature of acropodite and tapering smoothly to acuminate tip; tibial process broad, spatulate in shape but with grooves and ridges forming several smooth edges, one irregularly scalloped, obscuring solenomerite in lateral view, continuing general curvature of acropodite, widening distad, anterior margin apically flattened and forming acuminate tip with caudal margin. Prostatic groove arising in pit in prefemur, running along medial sides of acropodite and solenomerite, opening terminally.

*Description of female.*—There are no samples of *D. sternolobus* with both males and females from the same locality, so there are no certifiable females of this species. The one described here was taken about 9 mi. NW of the locality in Talladega Co. where a male was collected and is identified as *D. sternolobus* instead of the proximal *D. talapoosa* on the basis of size, since *D. sternolobus* is much larger than the latter. Length 39.9 mm, maximum width 8.4 mm, W/L ratio 21.0%, depth/width ratio 69.0%. Agreeing essentially with holotype in somatic features with following exceptions: Paranota more strongly depressed, creating appearance of more highly arched body; without sternal projections comparable to pregonopodal processes of male; postgonopodal sternal elevations of male absent, female sterna flat.

Cyphopods in situ with valvular openings visible in aperture. Receptacle absent. Valves relatively large, subequal, surfaces finely granuate. Operculum relatively large, located under lateral end of valves.

*Variation.*—There is considerable variation in the size of the sternal projections, one of the prime diagnostic features of the species. The one on segment 4, between the 3rd leg pairs, is highly variable and largest on the holotype. In the Shelby County males, this lobe is reduced to two widely separated knobs that are subequal in length to the adjacent coxal widths. The process between the anterior legs of segment 5 (4th legs) is less variable but still smaller than that of the holotype in the Talladega County male and the one from near Montevallo.

On the gonopods the prefemoral processes are relatively uniform, some curving less than others. The acropodite of the Talladega County male is more linear and massive, and the solenomerite is twisted so that the groove crosses to the lateral side about midlength of the structure. On the non-type males, the tibial process is produced apically into a subacute tip.

*Ecology.*—The male I collected in Shelby County was taken in a valley in a mesic hardwood forest not far from a creek.

*Distribution.*—Known only from six localities in the southern extremity of the Ridge and Valley Province in central Alabama. Most sites lie between US highways 280 and I-65, but the species probably occurs in adjacent counties in all directions. Specimens were examined as follows:

ALABAMA: *Shelby Co.,* Oak Mountain St. Pk., M, 22 May 1980, R. M. Shelley (NCSM A3130); and 7.3 mi. NW Montevallo, M, 29 Dec 1962, collector unknown (FSCA). *Coosa Co.,* 10 mi. N Rockford, M, F, 20 Apr 1983, R. M. Shelley and P. B. Nader (NCSM A4034). *Talladega Co.,* 2.8 mi. NW Sylacauga, 2F, 6 May 1954, L. Hubricht (RLH); and 6 mi. SE Sylacauga, M, 7 May 1975, L. Hubricht (RLH). *Tallapoosa Co.,* Alexander City, M, 27 Nov 1944, collector unknown (NMNH) TYPE LOCALITY.

*Remarks.*—Loomis (1969) was correct in stating that *D. sternolobus* was the largest species of *Dicellarius.* However, his remark about a sternal lobe between the 6th legs is somewhat misleading. This structure is more of a narrow transverse ridge, divided medially, than a ventrally produced, apically tapering lobe.

The affinities of *D. sternolobus* are unclear, but as in *D. b. lamellidens,* the acropodite curves caudomediad in situ and the solenomerite overlies the tibiotarsus in medial view. Perhaps *D. sternolobus* also evolved from a form of *D. bimaculatus* that became reproductively isolated in central Alabama, in similar fashion to the evolution of *D. okefenokensis* in southeastern Georgia and Florida.

## Genus *Thrinaxoria* Chamberlin and Hoffman

*Thrinaxoria* Chamberlin and Hoffman, 1950:4; 1958:51.

*Type-species.*—*Fontaria lampra* Chamberlin, 1918, by original designation.

*Description.*—A genus of moderate-size xystodesmids with the following characteristics:

Body composed of head and 20 segments in both sexes. Head of normal appearance, moderately smooth and polished. Antennae moderately slender, becoming progressively more hirsute distally, with 4 conical sensory cones on ultimate article; no other sensory structures apparent. Facial setae with or without epicranial, frontal, and genal series, with clypeal, and labral series; without interantennal and subantennal series.

Terga finely granulate, not polished; paranota moderately coriaceous. Collum moderately broad, ends subequal to those of following tergite. Paranota flattened to moderately depressed, interrupting slope of dorsum, caudolateral corners rounded on anteriormost segments, becoming blunt in midbody regions and progressively more acute posteriorly. Peritremata distinct, strongly elevated above metazonal surface; ozopores located caudal to midlength, opening dorsolaterad. Prozonites smaller than metazonites; strictures moderately distinct, slightly costulate.

Caudal segments normal for family.

Sides of metazonites granulate, without grooves or impressions. Gonapophyses broad, apically expanded. Pregonopodal sterna modified as follows: that of segment 4 with minute projection, much shorter than widths of adjacent coxae; that of segment 5 with small variable lobes or low transverse ridges between 4th legs and slight impression between 5th legs; that of segment 6 with impressions between both leg pairs. Postgonopodal sterna mildly hirsute, with or without low midline elevations. Coxae without projections; prefemoral spines relatively long and sharply pointed; tarsal claws slightly bisinuate. Hypoproct broadly rounded; paraprocts with margins slightly thickened.

Gonopodal apertures ovoid to elliptical. Gonopods in situ with apices crisscrossing in midline over 6th sternum. Coxae moderate in size, without apophyses, connected by membrane only, no sternal remnant. Prefemora moderate, with variable prefemoral processes arising on anterior or anteriomedial sides, either angling across acropodite stem or extending linearly along anterior margin. Acropodites moderately thick and robust, configurations variable, either bent strongly mediocaudad at midlength (level of distal division), slightly curved, or nearly linear; divided near ½ length into variable solenomerite and tibial process, continuous or discontinuous with axis of acropodite. Prostatic grooves arising in pits in bases of prefemora, running entirely along medial sides of acropodites onto solenomerites, opening terminally.

Cyphopodal apertures elliptical, encircling 2nd legs, sides slightly elevated above metazonal surfaces, without pleurotergal lobes on anteriolateral corners. Cyphopods in situ located lateral to 2nd legs, variably positioned in apertures. Receptacles varying from remnant to moderate structure cupped around part of valves, surfaces irregular, with slight lobes. Valves moderate and subequal, variously oriented in aperture, surfaces finely granulate. Opercula large, located under lateral end of valves.

*Distribution.*—Northwestern Louisiana to central Georgia, ranging northward into southwestern North Carolina (Blue Ridge Province) and west-central and southeastern Tennessee, and southward into the Coastal Plains of Alabama and Georgia. The Tennessee River is a distributional barrier in Tennessee and Alabama, as *T. lampra* has not been encountered in the Nashville Basin and Highland Rim Provinces on the "inside" of the loop as has *Pachydesmus* (Hoffman 1958). This barrier effect of the Tennessee River is interesting since the genus spans many large rivers, most notably the Mississippi.

*Species.*—Two, distinguished by the characters set forth in the following diagnoses.

*Thrinaxoria lampra* (Chamberlin)
Figs. 24–26

*Fontaria lampra* Chamberlin, 1918:371–372.
*Thrinaxoria lampra.*—Chamberlin and Hoffman, 1950:4; 1958:52.—Causey, 1963:77.
*Zinaria aberrans* Chamberlin, 1942:4, pl. 1, fig. 7.

*Type-specimens.*—Male paratypes (RVC, RLH) taken by K. P. Schmidt, 9 Mar 1915, from Creston, Natchitoches Par., Louisiana. The male holotype, collected at this locality on 26 Mar 1915 (Chamberlin 1918) and reported to be in the MCZ (Chamberlin and Hoffman 1958), is lost, since it is not at Harvard nor in the Chamberlin collection. Two female paratypes from Creston, supposedly of *T. lampra,* are in the MCZ, but they were taken on 5 Mar 1915 the same date that the type of *Pachydesmus clarus* (Chamberlin) was collected there (Chamberlin 1918). Since the features of females of *T. lampra* and *P. clarus* are nearly identical, it is impossible to tell which species these females belong to.

*Diagnosis.*—Prefemoral process short, angling across stem of acropodite; distal elements bent abruptly caudomediad, discontinuous with general curvature of acropodite; cyphopods with moderate receptacle.

*Paratype.*—Length 35.5 mm, maximum width 7.2 mm, W/L ratio 20.3%, depth/width ratio 61.1%. Segmental widths as follows:

| | | | |
|---|---|---|---|
| collum | 6.2 mm | 16th | 6.9 |
| 2nd | 6.8 | 17th | 6.1 |
| 3rd | 7.0 | 18th | 4.6 |
| 4th–15th | 7.2 | | |

Color in life unknown.

Head capsule smooth, polished; width across genal apices 4.2 mm, interantennal isthmus 1.6 mm; epicranial suture thin but distinct, terminating above interantennal region, not bifid. Antennae moderately long, reaching back to middle of 4th segment, relative lengths of antennomeres $2 > 3 > 4 = 5 = 6 > 1 > 7$. Genae not margined laterally, with distinct, linear, central impressions, ends broadly rounded and projecting slightly beyond adjacent cranial margin. Facial setae as follows: Epicranial 2-2, interantennal absent, frontal 1-1, genal 2-2, clypeal about 12-12, labral about 22-22.

Collum relatively broad, ends not extending beyond those of adjacent tergite. Dorsum finely granulate, not polished. Paranota relatively flattened, interrupting slope of dorsum and subparallel to substrate, anterior corners rounded through segment 5, becoming blunt and progressively more acute posteriorly. Peritremata distinct, strongly elevated above paranotal surface. Ozopores located caudal to midlength of peritremata, opening dorsolaterad.

Sides of metazonites dull and granulate but without noticeable grooves or impressions. Strictures sharp, distinct, prozona elevated slightly above metazona. Sternum of segment 4 with minute projection; that of segment 5 with two low, widely separated, transverse ridges between 4th legs and with slight impression between 5th legs (Fig. 24); 6th sternum with distinct impressions between both leg pairs. Postgonopodal sterna flattened, without trace of midline elevations; caudal margins indented medially.

Gonopodal aperture ovoid, 2.2 mm wide and 1.2 mm long at midpoint, without anteriolateral indentations, sides flush with metazonal surface. Gonopods in situ (Fig. 25, not this specimen) with acropodites projecting anteriad and bending mediad, apices crisscrossing in midline over 6th sternum; prefemoral processes extending mediad and overlapping at midlength, tips projecting just beyond anterior margin of aperture. Gonopod structure as follows (Fig. 26): Prefemoral process short, terminating well below distal division of acropodite, angling across stem of acropodite and directed toward distal extremity of tibial process. Acropodite bent sharply mediocaudad at level of distal division, distal elements discontinuous with curvature of acropodite, overhanging and extending well beyond level of prefemur; stem relatively narrow and parallel-sided proximal to bend. Distal elements widely separated by subovoid space, converging apically, directed generally mediocaudad; tibial process slightly longer and more proximal, with slight basal curve, flattened distally and produced into blunt tip; solenomerite flattened basally, sides roughly parallel then tapering and curving apically to blunt tip, tip directed toward tibial process. Prostatic groove arising in pit in prefemur, running entirely along medial side of acropodite onto solenomerite, opening terminally.

*Female topotype.*—Length 35.0 mm, maximum width 6.3 mm, W/L ratio 18.0%, depth/width ratio 76.2%. Agreeing essentially with males in somatic features except paranota much more strongly depressed, angling sharply ventrad, creating appearance of more highly arched body; without trace of sternal elevations.

Cyphopods in situ with corner of valves and receptacle visible in aperture. Receptacle cupped around medial end of valves, surface moderately irregular and rugulose, with slight lobes. Valves moderate and subequal, oriented subperpendicularly to body axis in aperture, surface finely granulate. Operculum large, located under lateral end of valves.

*Variation.*—The sternal ridges between the 4th legs of segment 5 vary and become lobe-like in Alabama, resembling their condition in *T. bifida.* The prefemoral processes of *T. lampra* are all short as in the holotype, in contrast to the variation in the congener.

*Distribution.*—*Thrinaxoria lampra* is known from two allopatric populations, a fairly continuous one in northwestern Louisiana and one with widely separated samples from west-central Tennessee to southwestern Alabama. In Alabama it occurs sympatrically and syntopically with *D. t. separandus* in Tuscaloosa and

*D. b. bimaculatus* along the Tombigbee River in Washington County. The Tennessee River constitutes a range boundary because the known localities are all on the "outside" of the loop formed by the river as it passes through Alabama and northward into western Tennessee. The species can be listed as probable for eastern Texas and southwestern Arkansas, since Miller County, Arkansas, and Cass, Marion, Harrison, Panola, and Shelby counties, Texas, are only a few miles from known localities in Caddo, Desoto, and Sabine Parishes, Louisiana. Thus, *T. lambra* becomes the third species whose occurrence in northeastern Texas can be predicted from distributions in adjacent states, the others being *Pleuroloma flavipes* Rafinesque and *Auturus l. louisianus* (Chamberlin) (Shelley 1980, 1982). Specimens were examined as follows:

LOUISIANA: *Caddo Par.,* 5 mi. NW Shreveport, M, 13 Apr 1936, L. Hubricht (RVC). *DeSoto Par.,* 11 mi. N Mansfield, 2M, 25 Aug 1966, R. E. Tandy (FSCA). *Sabine Par.,* 8 mi. W Noble, M, 5 Apr 1969, D. C. Marizot and R. M. Blaney (FSCA). *Red River Par.,* 4 mi. NW Coushatta, M, 10 Apr 1971, P. Kimmick (FSCA). *Natchitoches Par.,* no further data, 2F, 22 Mar 1957 and 20 Apr 1961, collector unknown (FSCA); Moreland, M, 16 Oct 1954, collector unknown (FSCA); and Creston, 2M, F, unknown date in 1915, K. P. Schmidt (RVC), M, 9 Mar 1915, K. P. Schmidt (RLH), and 2M, 2F, 26 Mar 1915, K. P. Schmidt (MCZ) TYPE LOCALITY.

TENNESSEE: *Henderson Co.,* Natchez Trace St. Pk., 2M, 3F, 26 May 1980, R. M. Shelley (NCSM A3159).

MISSISSIPPI: *Tishomingo Co.,* Tishomingo St. Pk., M, 15 May 1964, L. Hubricht (RLH).

ALABAMA: *Walker Co.,* Jasper, 800 Airport Rd., 3M, 21 Jun 1975, B. R. Wall (NCSM A596), and M, 29 Apr 1978 (NCSM A2591). *Tuscaloosa Co.,* Tuscaloosa, M, F, 29 Mar 1948, G. E. Ball (RLH) and 2M, 3F, tunneling in Zoyzia grass, 13 Apr 1982, E. A. Cross (NCSM A3933). *Washington Co.,* 3 mi. E Leroy, near Tombigbee R., M, F, 3 Jul 1960, L. Hubricht (RLH) and M, 28 Apr 1983, R. M. Shelley and P. B. Nader (NCSM A4048).

*Remarks.*—Because of the general gonopodal similarity with *Pleuroloma flavipes, T. lampra* was described as a species of *Zinaria* (now a synonym of *Pleuroloma*) by Chamberlin (1942). This similarity is merely coincidental, however, and a relationship between *Thrinaxoria* and *Pleuroloma* was discounted by Chamberlin and Hoffman (1950) and Shelley (1980).

*Thrinaxoria bifida* (Wood), new combination
Figs. 27–28

*Polydesmus* (*Fontaria*) *bifidus* Wood, 1864:7; 1865:223, fig. 52.
*Epeloria bifida.*—Chamberlin and Hoffman, 1958:32.

*Type-specimen.*—As stated in the introduction, Wood's types are lost. I therefore designate a neotype as follows: Male neotype (NCSM A2339) collected by R. M. Shelley and W. B. Jones, 8 Jul 1978, along road to Chilowhee Campground, 1.9 miles NW of the junction with US highway 64, 0.2 miles NE Parksville, Polk Co., Tennessee. The other specimens from Polk Co. in the locality listing are designated neoparatypes.

*Diagnosis.*—Prefemoral process variable, short to long, usually extending linearly along anterior margin of acropodite stem, rarely angling across latter; distal elements continuous with and continuing overall curvature of acropodite; cyphopods with remnant of receptacle.

*Neotype.*—Length 35.8 mm, maximum width 7.8 mm, W/L ratio 21.2%, depth/width ratio 64.1%. Segmental widths as follows:

| | | | |
|---|---|---|---|
| collum | 6.7 mm | 14th–15th | 7.4 |
| 2nd | 6.9 | 16th | 7.2 |
| 3rd | 7.1 | 17th | 6.8 |
| 4th | 7.6 | 18th | 5.5 |
| 5th–13th | 7.8 | | |

Color in life: Dorsum generally bright orange in color, with darker and lighter hues blending across metaterga.

Somatic features similar to those of *T. lampra,* with following exceptions:

Width across genal apices 4.5 mm, interantennal isthmus 1.1 mm. Antennae reaching back to middle of 4th tergite, relative lengths of antennomeres $2 > 3 > 4 = 5 = 6 > 1 > 7$. Genae with slight central impressions. Facial setae as follows: Epicranial, interantennal, frontal, and genal not detected and presumed absent, clypeal about 10-10, labral about 15-15.

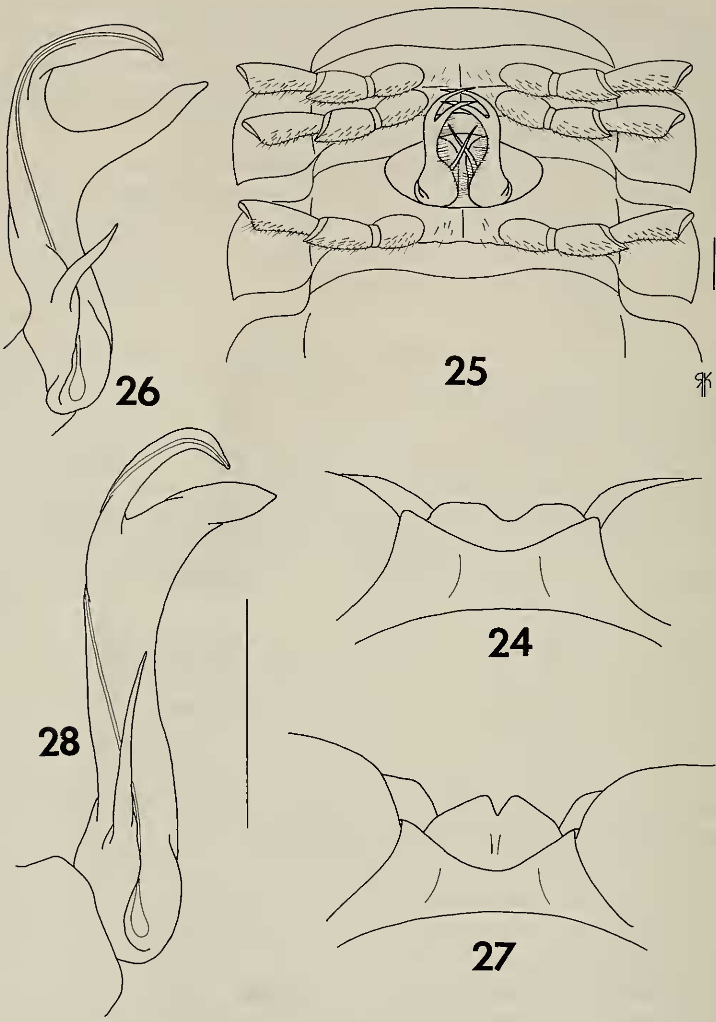
Collum broad, ends extending well below those of following tergite. Peritremata relatively indistinct, only slightly elevated above paranotal surface.

Sternum of segment 5 with two apically separated paramedial lobes between 4th legs, height subequal to widths of adjacent coxae, and with moderate recession between 5th legs (Fig. 27); 6th sternum convexly recessed between both legs, 7th legs set slightly farther apart than 6th. Postgonopodal sterna with low, almost indetectable, longitudinal elevations on segments 8-15.

Gonopodal aperture elliptical, 2.6 mm wide and 1.3 mm long at midpoint, indented anteriolaterally, sides elevated above metazonal surface. Gonopods in situ with acropodites extending anteriad from aperture, distal elements curving mediad and crossing those of opposite member in midline over 6th sternum. Gonopod structure as follows (Fig. 28): Prefemoral process moderately long but terminating well below distal division of acropodite, angling slightly across stem of acropodite but not crossing caudal margin. Acropodite curving gradually mediocaudad at midlength proximal to distal division, distal elements continuous with curvature and acropodite stem, extending well beyond level of prefemur; stem relatively narrow and parallel-sided basally, sides diverging gradually at beginning of curve. Distal elements separated by moderate space, generally diverging and directed mediocaudad; tibial process longer and more proximal, broad and laminate, apically subacute; solenomerite with sides parallel, continuing curvature of acropodite but bent abruptly dorsad distally, tip directed toward tibial process. Prostatic groove arising in pit in prefemur, running entirely along medial side of acropodite onto solenomerite, opening terminally.

*Description of females.*—Since no females have been taken in Polk County, Tennessee, a composite description of their characters has been prepared from the three specimens in adjacent Cherokee County, North Carolina.

Length 37.7 mm, maximum width 7.1 mm, W/L ratio 18.8%, depth/width ratio 73.2%. Agreeing closely with males in somatic features except paranota more




Figs. 24–28. *Thrinaxoria* spp. 24–26, *T. lampra*: 24, Sternum of segment 5 of paratype, caudal view; 25, Gonopods in situ, ventral view of male from Henderson Co., TN; 26, Telopodite of left gonopod of paratype, medial view. 27–28, *T. bifida*: 27, Sternum of segment 5 of neotype, caudal view; 28, Telopodite of left gonopod of the same, medial view. Scale line for Fig. 25 = 1.00 mm; line for other Figs. = 1.33 mm for 24 and 27, 1.00 mm for 26, and 1.14 mm for 28.

strongly depressed, creating appearance of more highly arched body, and without trace of sternal elevations.

Cyphopods in situ with opening of valves directed ventrad. Receptacle much smaller than in *T. lampra,* a thin darkened remnant of tissue located mediad or anteromediad to the valves. Valves moderate and subequal, surface finely granulate. Operculum large, located under lateral end of valves.

*Variation.*—The prefemoral processes vary, and in males from Whitfield and Dougherty counties, Georgia, they are long and acicular, projecting beyond the division of the acropodite. In most males this structure is linear and directed

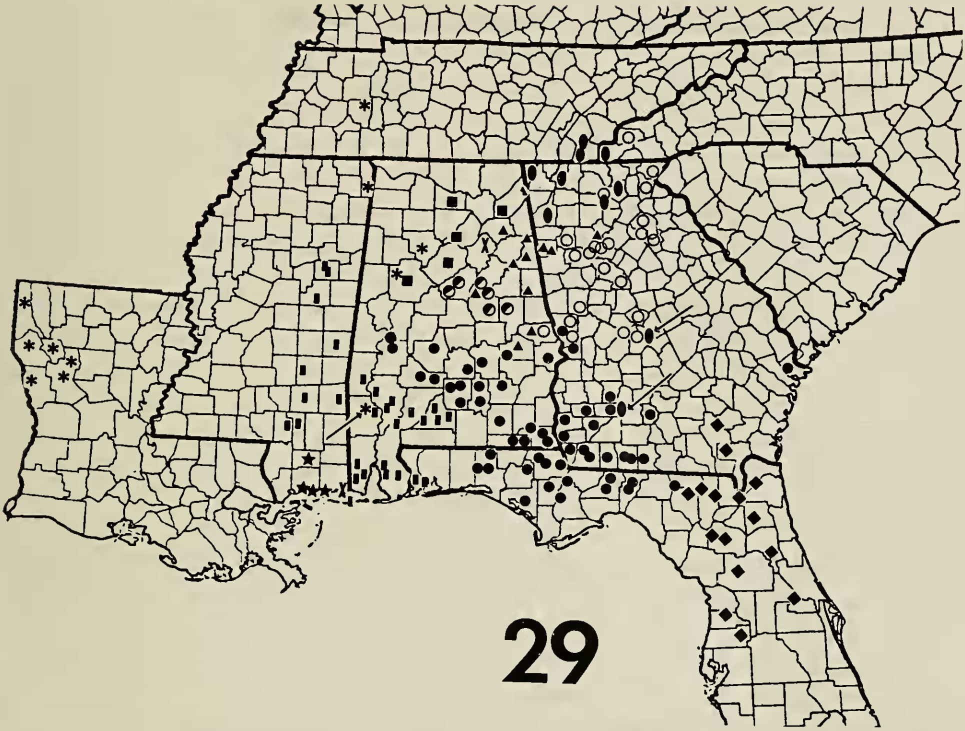



Fig. 29. Distribution of *Dicellarius* and *Thrinaxoria.* rectangles, *D. b. bimaculatus*; dots, *D. b. fictus*; stars, *D. b. lamellidens*; lower X, *D. bimaculatus* intergrades; triangles, *D. t. talapoosa*; squares, *D. t. separandus*; upper X, *D. talapoosa* intergrades; circles, *D. atlanta*; half shaded circles, *D. sternolobus*; diamonds, *D. okefenokensis*; asterisks, *T. lampra*; ovals, *T. bifida.* The arrows indicate apparently isolated populations of the species of *Thrinaxoria* within the range of *Dicellarius.*

along the anterior margin of the acropodite. The neotype is thus an exception in having the process angle across the stem. In other males from Polk County the distal elements are more widely separated, and the solenomerite is broadly curved toward the tibial process instead of being abruptly bent. The overall curvature of the acropodite is similar in all males, but the solenomerite in the one from Dougherty County is nearly upright, with only a slight apical bend. The elements are thus more widely separated so that the overall configuration resembles that of *D. atlanta.*

*Distribution.*—Southern extremity of the Blue Ridge and Ridge and Valley Provinces to the Coastal Plain, from southeastern Tennessee and southwestern North Carolina to southern Georgia. Specimens were examined as follows:

TENNESSEE: *Polk Co.,* 6.5 mi. NE Benton, Chilowhee Rec. Area, Cherokee Nat. For., M, 20 Jun 1950, L. Hubricht (RLH); Oswald Dome, Bean's Mtn., 2M, 12 Jun 1953, L. Hubricht (RLH); and 0.2 mi. NE Parksville, along rd. to Chilowhee Cpgd., 1.9 mi. NW jct. US hwy. 64, M, 8 Jul 1978, R. M. Shelley and W. B. Jones (NCSM A2339) NEOTYPE LOCALITY.

NORTH CAROLINA: *Cherokee Co.,* Wolf Creek vic., ca. 1 mi. E TN st. line, F, 16 May 1979, R. M. Shelley and R. K. Tardell (NCSM A2706); and 6 mi.

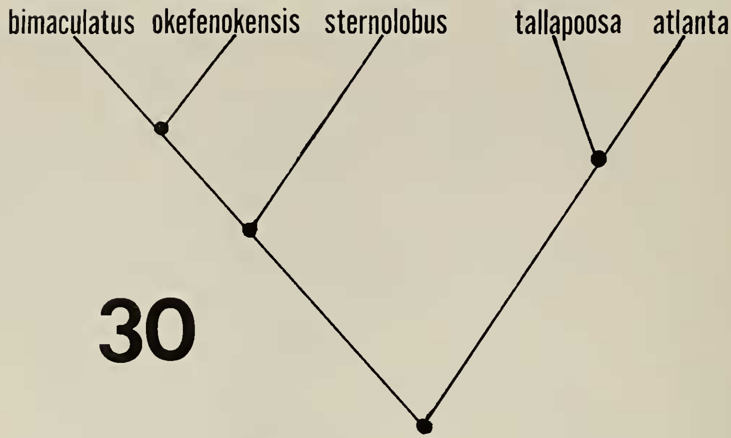



Fig. 30. Relationships in *Dicellarius.*

WNW Culberson, along co. rd. 1107, 0.2 mi. N jct. co. rd. 1108, F, 27 Jul 1974, R. M. Shelley (NCSM A2405) and F, 6 Jul 1978, R. M. Shelley and W. B. Jones (NCSM A2330).

GEORGIA: *Dade Co.,* Cloudland Canyon St. Pk., F, 27 Apr 1979, R. M. Shelley (NCSM A2607). *Whitfield Co.,* Dalton, along creek off I-75 at jct. GA hwy. 52, M, 16 Apr 1978, R. M. Shelley and R. E. Ashton (NCSM A1847). *Dawson Co.,* along Amicalola River, 1.5 mi. E Amicalola Falls, M, 15 Apr 1961, L. Hubricht (RLH). *Lumpkin Co.,* 16 mi. NW Dahlonega, M, F, 17 Jun and 2 Jul 1973, A. LaVallee and R. Duffield (RLH). *Floyd Co.,* Rome vic., F, 13 Oct 1954, P. J. Darlington (RLH). *Houston Co.,* Perry, M, 26–28 Dec 1982, J. A. Payne (RLH). *Dougherty Co.,* 8.4 mi. S Albany, just inside Mitchell Co. line on GA hwy. 3, M, 15 Sep 1979, R. M. Shelley and P. T. Hertl (NCSM A2877).

## Relationships

At present I cannot resolve the generic relationships in the Pachydesmini. Of the three other eastern xystodesmid tribes, the Apheloriini is chosen as the out-group because of the synapomorphic absence of a sternal remnant between the gonopodal coxae. The genera of the Rhysodesmini possess such a remnant, a plesiomorphic trait, and the Nannariini, with small size, modified tarsal claws anteriorly in males, and subcoxal sternal spines, is clearly a derived, specialized group. Since apheloriine diplopods have a receptacle on the cyphopods, *Pachydesmus,* which possesses this structure, could be considered sister to *Thrinaxoria,* which has a vestigial to moderate receptacle, and *Dicellarius,* which lacks the feature. However, since apheloriines have generally unmodified midbody sterna, *Thrinaxoria,* which has the most poorly developed elevations, could be considered sister to *Dicellarius* and *Pachydesmus.* These seem the only useful characters to resolve the question because others are not shared significantly with the out-group. For example, very few apheloriine taxa have a divided acropodite, and the coxal apophyses are autapomorphous in both *Pachydesmus* and *Deltotaria.* Consequently, until other features are discerned that clarify this matter, the relationships in the Pachydesmini are best considered an unresolved trichotomy.

Within *Dicellarius* there are two obvious branches based primarily on the configurations of the tibial processes. One line leads to *D. talapoosa* and *D. atlanta,* in which the process tapers continuously to a subacuminate tip, and the other leads to *D. bimaculatus, D. okefenokensis,* and *D. sternolobus,* in which it is broad for most of its length, narrowing only near the tip. These two lineages are geographically plausible, since their members are situated proximally to each other (Fig. 29). The key species appear to be *D. bimaculatus* and *D. talapoosa*; the others appear to represent segregated populations of these that have achieved reproductive isolation. *Dicellarius atlanta* is very similar to forms of *D. talapoosa,* but their overlapping ranges are proof of reproductive isolation. Similarly, the acropodal curvature of *D. okefenokensis* is an augmentation of that exhibited by eastern populations of *D. bimaculatus* (*b. fictus*), and the torsion culminates the west to east, counterclockwise to clockwise, rotation cline of the latter. These observations suggest that *D. okefenokensis* was once connected to *D. bimaculatus* by intergrades that have disappeared, leaving it reproductively isolated. Less conclusive evidence is available for *D. sternolobus,* but its caudally curved acropodite and the overlying of the tibiotarsus by the narrow solenomerite in medial view are similar to the conditions in *D. b. lamellidens.* Since this pattern exists in known populations of *D. bimaculatus,* it could also have evolved a second time in interior populations that are now fully isolated. These ideas on relationships are depicted in Fig. 30.

## Acknowledgments

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